A NEW GENUS AND FIVE NEW SPECIES OF MUSSELS (BIVALVIA, MYTILIDAE) FROM DEEP-SEA SULFIDE/HYDROCARBON SEEPS IN THE GULF OF MEXICO

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ABSTRACT

Five new species of modioliform mussels in the family Mytilidae are described from material collected at sulfide/hydrocarbon seeps in the Gulf of Mexico. New definitive taxa, placed in the subfamily Bathymodiolinae, include the genus Tamu and the species Tamu fisheri from hydrocarbon seeps on the Louisiana Continental Slope, Bathymodiolus heckerae from brine seeps at the base of the West Florida Escarpment in the eastern Gulf of Mexico, and Bathymodiolus brooksi from the West Florida Escarpment site and from hydrocarbon seeps at Alamiños Canyon in the western Gulf of Mexico. An additional two new mussel species, which exhibit combinations of morphological characters unlike any existing mytilid genus but for which molecular data are equivocal, are provisionally placed in the genera Bathymodiolus and Idas, respectively. These are: "Bathymodiolus" childressi from hydrocarbon seeps at Alamiños Canyon and the Louisiana Continental Slope, and "Idas" macdonaldi (in the subfamily Modiolinae) from hydrocarbon seeps on the Louisiana Continental Slope.

Key words: Mytilidae, deep-sea, sulfide seeps, hydrocarbon seeps, Bathymodiolinae.

INTRODUCTION

Modioliform mussels in the family Mytilidae are conspicuous members of many deep-sea hydrothermal vent and cold-water methane/sulfide seep environments. A common feature of these mussels is their dependence on sulfide-oxidizing or methanotrophic symbionts (Fisher, 1990; Cavanaugh, 1992). The first vent mussel described was Bathymodiolus thermophilus Kenk & Wilson, 1985, which occurs at hydrothermal vents on the Galápagos Rift and the East Pacific Rise (EPR). Recently described species are: B. platifrons Hashimoto & Okutani, 1994; B. japonicus Hashimoto & Okutani, 1994; B. aduloides Hashimoto & Okutani, 1994; and B. septemdierum Hashimoto & Okutani, 1994, from vent and cold seep sites around Japan; B. brevior Cosel, Métivier & Hashimoto, 1994, and B. elongatus Cosel, Métivier & Hashimoto, 1994, from vent sites in the south Pacific; and B. puteoserpentis Cosel, Métivier & Hashimoto, 1994, from the Snake Pit site on the Mid-Atlantic Ridge. In addition, the small mussel Idas washingtonia (Bernard, 1978) occurs at hy-

drothermal vents on the Juan de Fuca Ridge in the north-eastern Pacific (Juniper et al., 1992) and Amygdalum politum (Verrill & Smith, in Verrill, 1880), a small thin-shelled mytilid, occurs near cold water hydrocarbon seeps on the Louisiana Continental Slope (Turner, 1985).

As yet undescribed modioliform mussels were reported from hydrothermal vents or cold-seeps in the Pacific Ocean at Guaymas Basin (Turner, 1985), Middle Valley (Juniper et al., 1992), the Mariana Back-Arc Basin (Hessler & Lonsdale, 1991), and the Mid-Okinawa Trough (Hashimoto et al., 1995); and in the Atlantic Ocean at the South Barbados accretionary prism (Jollivet et al., 1990) and on the Mid-Atlantic Ridge at 37°50′N ("Menez Gwen" site), 37°17′N ("Lucky Strike" site), 29°N ("Broken Spur" site), and 14°45′N (Cosel et al., 1997).

An allozyme survey by Craddock et al. (1995) identified several additional modioliform taxa from sulfide/hydrocarbon seeps in the Gulf of Mexico. A subsequent analysis of these specimens for DNA sequences from a region of the mitochondrial Cytochrome c Ox-

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TABLE 1. New species and type localities of modioliform mussels from the Gulf of Mexico.

New species	Location	Latitude Longitude	Depth (m)
Bathymodiolus heckerae	West Florida Escarpment	26°02.2' N 84°54.5' W	3314
Bathymodiolus brooksi	Alamiños Canyon	26°21.3' N 94°29.7' W	2222
Bathymodiolus brooksi	West Florida Escarpment	26°02.2' N 84°54.5' W	3314
"Bathymodiolus" childressi	Bush Hill, Louisiana Continental Slope	27°46.9' N 91°30.4' W	546
"Bathymodiolus" childressi	Brine Pool-NR 1, Louisiana Continental Slope	27°43.4' N 91°16.6' W	650
"Bathymodiolus" childressi	Alamiños Canyon 26°21.3' N, 94°29.7' W		2222
Tamu fisheri	Bush Hill, Louisiana Continental Slope	27°46.9' N 91°30.4' W	546
Tamu fisheri	Near Garden Banks-386, Louisiana Continental Slope	27°50' N 92°10' W	650
"Idas" macdonaldi	Near Garden Banks-386, Louisiana Continental Slope	27°50' N 92°10' W	650

idase Subunit-I (COI) gene corroborated the discrete nature of these taxa (W. R. Hoeh, pers. comm., unpublished data).

Herein, we describe five of the mytilid species identified in Craddock et al. (1995) from the Gulf of Mexico (Table 1, Fig. 1). Following the suggestion of Soot-Ryen (1955), characters used for classification of these new mytilid species have been taken from the shell or from easily visible parts of the anatomy, such as muscles, gill, and mantle margins. Of special importance to classification in the Mytilidae is the comparative placement of the retractor muscles of the foot and byssus (Soot-Ryen, 1955; Knudsen 1970). However, where deemed important, taxonomic characters associated with the internal anatomy, such as the course taken by the digestive tract, have been included.

MATERIALS AND METHODS

Specimens

Mussel specimens were collected during dives of the DSV ALVIN (A) and DSRV JOHNSON SEA-LINK-I (JSL) (Tables 1–7) and subsequently prepared as described in Craddock et al. (1995). Additional specimens were provided by Colleen M. Cavanaugh (Harvard Univ.), James J. Childress (Univ. California – Santa Barbara), Charles R. Fisher (Pennsylvania State Univ.), Ian R. MacDonald (Texas A & M Univ.), and Craig R. Smith (Univ. Hawaii – Manoa).

Holotypes and a series of paratypes are deposited in the Academy of Natural Sciences of Philadelphia (ANSP). Additional paratypes are deposited in the following institutions: United States National Museum of Natural History, Washington, D.C. (USNM); Museum of Comparative Zoology, Harvard University (MCZ); Houston Museum of Natural Science, Houston, Texas (HMNS), Museum National d'Histoire Naturelle, Paris (MNHN), and Rutgers University (RU). Catalogue numbers and other pertinent information concerning holotypes and paratypes are summarized in Appendix 1.

Shell and anatomical features of specimens of the following species were examined for this report: Bathymodiolus thermophilus and B. puteoserpentis from their respective type localities; paratypes of Benthomodiolus abyssicola (Knudsen, 1970) borrowed from ZMUC; Idas argenteus Jeffreys, 1876, from the Tongue of the Ocean (TOTO) east of Andros Island in the Bahama Islands; Idas washingtonia from South Cleft hydrothermal vent on the Juan de Fuca Ridge off southern British Columbia and from whale bone in the Santa Catalina Basin off California; Adipicola sp. from Middle Valley on the Juan de Fuca Ridge; and undescribed deep-sea mussels from Mariana Back-Arc Basin in the Pacific and Lucky Strike on the Mid-Atlantic Ridge.

Small shells examined by scanning electron microscopy were air dried, glued to stubs, coated with approximately 400 A of gold/palladium, and viewed on an Hitachi S-450 scanning electron microscope. Drawings of shells
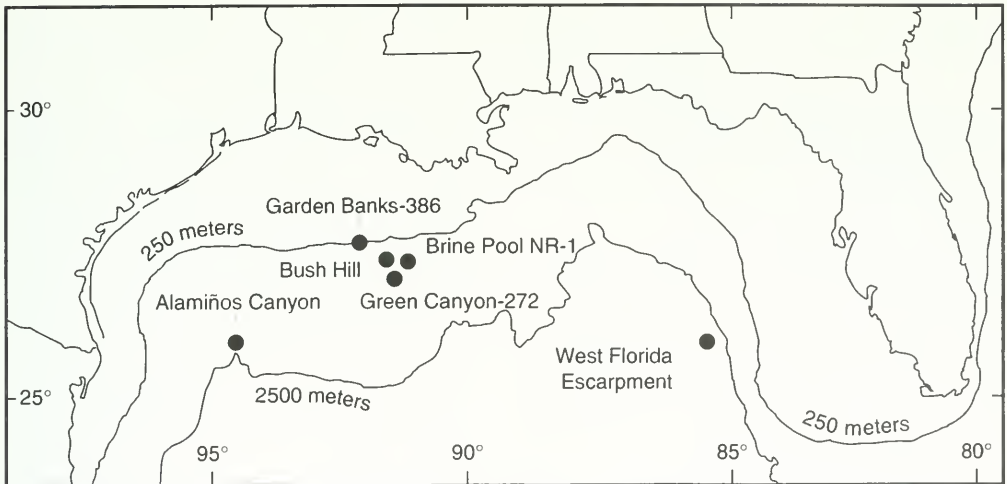
FIG. 1. Location of submersible dive sites in the Gulf of Mexico where mussels were collected.

and tissues were made either freehand or with the aid of a camera lucida.

Morphological Terminology

The "horizontal branchial septum" is a thin, membranous horizontal shelf separating incurrent and excurrent chambers, posterior to the posterior adductor (commonly extends from the ventral side of posterior adductor to the base of the excurrent siphon). The "valvular siphonal membrane" is an extension of the branchial septum formed by fusion of right and left mantle lobes ventral to the excurrent siphon and extending a variable distance into the pedal-byssal gape; a small centrally placed papilla is sometimes present at the anterior end of the valvular siphonal membrane.

Morphometrics

Shell measurements used to statistically discriminate among the five new species were: L = length of valve; H = height of valve; W = width of valves, G = length of the ligament; and A = anterior length or the distance from the anterior shell margin to an imaginary line drawn vertically from the anterior edge of the beak or umbonal bulge (Fig. 2). Measurements were made with hand-held calipers (±0.1 mm). All analyses were performed on log10 transformations of the original variables. Multivariate analyses were performed on standardized variables with Varimax rota-

tion using the statistical computer program JMP 3.0.2 (SAS Statistics Inst., Inc, Raleigh, North Carolina).

SYSTEMATIC SECTION

Family Mytilidae

Subfamily Bathymodiolinae Kenk & Wilson, 1985
Type genus: Bathymodiolus Kenk & Wilson, 1985

Revised Diagnosis: Shell smooth, modioliform, with subterminal umbones; adult hinge edentulous, juvenile hinge with small denticulations anterior and posterior of ligament; posterior byssal retractors divided into anterior and posterior portions with separate insertion points on the adult shell producing separate muscle scars; intestine short, either straight or with a very short recurrent loop; demibranchs of hypertrophied ctenidia thick and fleshy, inner and outer demibranchs of equal length, filaments broadly thickened. Ctenidia associated with symbiotic bacteria.

Remarks: As originally described this subfamily contained the single genus Bathymodiolus (Kenk & Wilson, 1985). Eight members of this subfamily have been previously described: B. thermophilus, B. brevior, B. elongatus, B. puteoserpentis, B. platifrons, B. japonicus, B. aduloides, and B. septemdierum (Kenk & Wilson, 1985; Hashimoto & Okutani, 1994; Cosel
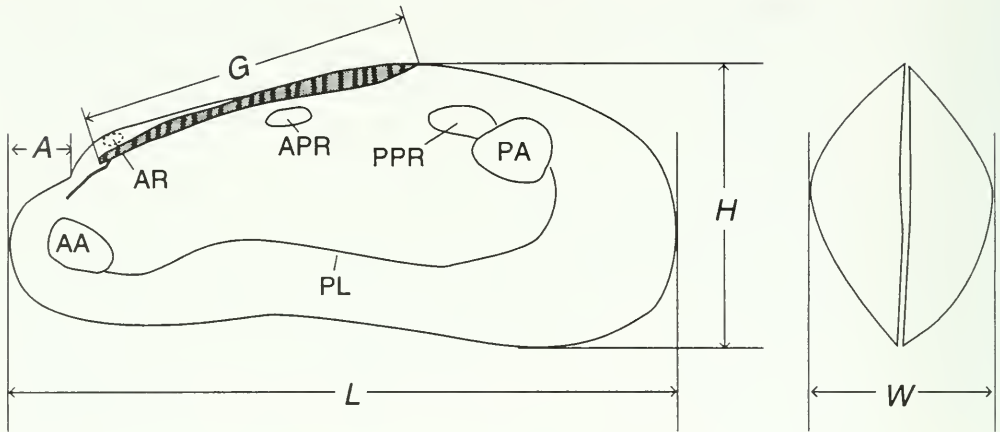
FIG. 2. Diagram depicting measurements taken and generalized shell characters. A, anterior length (distance from anterior shell margin to anterior edge of umbo); AA, anterior adductor; APR, anterior portion of posterior byssal-pedal retractor; AR, anterior byssal-pedal retractor; H, shell height; L, shell length; G, ligament length; PA, posterior adductor; PL, pallial line; PPR, posterior portion of posterior byssal-pedal retractor; W, width of shell valves.

et al., 1994). The current contribution adds the genus Tamu and the species T. fisheri, B. heckerae, and B. brooksi to the subfamily.

All members of this subfamily have hypertrophied gills associated with symbiotic bacteria that reside either within certain cells termed "bacteriocytes" or on the gill surface (Fisher, 1990; Fisher et al., 1993; Cavanaugh, 1992; Cavanaugh et al., 1987; C.M. Cavanaugh, pers. comm.). The simplified alimentary system, hypertrophied gills, and symbiosis with sulfide-oxidizing or methanotrophic bacteria, indicative of a different feeding mechanism in this group, separates members of this subfamily from all other known mytilids.

Bathymodiolus Kenk & Wilson, 1985

Bathymodiolus LePennec et al. 1983: 70; Le Pennec & Hily, 1984: 517; Laubier & Desbruyères, 1984: 1507; Smith, 1985: 1068 [nomen nudum].
Bathymodiolus Kenk & Wilson, 1985: 255 (type species, by original designation, Bathymodiolus thermophilus Kenk & Wilson, 1985).

Revised Diagnosis: Shell large (maximum size greater than 90 mm), smooth, modioliform, with sub-terminal umbones; adult hinge edentulous, juvenile hinge with small denticulations anterior and posterior of ligament (Figs. 3–5); posterior byssal retractors divided into posterior and anterior portion, retractor scars separate; labial palp suspensors and pedal retractors present; demibranchs of ctenidia thick and fleshy; filaments broadly thickened, with reduced ventral food grooves, containing intracellular bacterial symbionts; intestine straight without recurrent loop; rectum enters ventricle anterior to the auricular ostia.

Remarks: The manuscript name Bathymodiolus was introduced as a nomen nudum by LePennec et al. (1983: 70) and subsequently appeared in Le Pennec & Hily (1984), Laubier & Desbruyères (1984), and Smith (1985; publication date, May) prior to its valid introduction, under the rules of the International Code of Zoological Nomenclature (ICZN), by Kenk & Wilson (1985; publication date, 9 July).

The extremely reduced pedal gape of B. thermophilus appears to be a derived character, absent in other species referred to this genus (Hashimoto & Okutani, 1994; Cosel et al., 1994, 1997). Bathymodiolus brevior, B. elongatus, B. puteoserpentis (Cosel et al., 1994), and "Bathymodiolus" childressi have been referred to Bathymodiolus on a provisional basis. The final systematic placement of these species, and others placed in Bathymodiolus, must await complete morphological analyses and molecular studies on the entire group of deep sea mytilids.

Bathymodiolus thermophilus Kenk & Wilson, 1985 Figures 3–5

Bathymodiolus thermophilis (sic) Laubier & Desbruyères, 1984: 1510 [nomen nudum].
Bathymodiolus thermophilus Smith, 1985 (May): 1068 [nomen nudum].
Bathymodiolus thermophilus Kenk & Wilson, 1985 (9 July): 255, figs. 2–13 (type locality, "Mussel Bed" hydrothermal vent, Galápagos Rift, 0°47.89'N; 86°9.21'W in 2495 m, ALVIN Dive 879; holotype USNM 803661).

Description: Shell large, up to 180 mm long, modioliform, with sub-terminal umbones, elliptical in juveniles, arcuate in older specimens. Ventral shell margin nearly straight in young specimens, slightly concave in specimens larger than 10 cm. Adult hinge edentulous, juvenile hinge with small denticulations anterior and posterior to ligament. Posterior byssal retractors divided, retractor scars separate; separate pedal retractors prominent; slender labial palp suspensors extend anteriorly from anterior retractors to support the muscularized labial palps. Ventral pallial line with a dorsally directed concavity in byssal region about one-third of the distance from the anterior end. Inner fold of mantle lobes fused in postero-ventral and antero-ventral midline creating valvular siphonal membrane, with papilla, and an extremely reduced pedal gape. Dorsal edges of ascending lamellae attached to muscular longitudinal ridges on surfaces of mantle lobe and visceral mass. Horizontal branchial septum, extending from the base of the excurrent siphon and the ventral side of the posterior adductor, separates incurrent and excurrent chambers posteriorly. Inner and outer demibranchs essentially equal-sized, thick and fleshy, filaments broadly thickened, with reduced ventral food grooves. Ctenidia contain intracellular symbiotic bacteria. Muscularized inner palps long and slender, attached over most of their length to visceral mass, extending farther posteriorly than smaller muscularized outer palps. Intestine straight without recurrent loop; intestine/rectum enters ventricle anterior to the position of the auricular ostia.

Remarks: The manuscript species name Bathymodiolus thermophilis (sic) was introduced as a nomen nudum by Laubier & Desbruyères (1984) and as B. thermophilus by Smith (1985; publication date, May) prior to the valid description of this species, under the rules of the ICZN, by Kenk & Wilson (1985; publication date, 9 July).

Kenk & Wilson (1985) described Bathymodiolus as having a small pedal gape resulting from extensive ventral fusion of the inner folds of the mantle lobes. This feature is present in the type species B. thermophilus, but is lacking in other described members of this genus (Hashimoto & Okutani, 1994; Cosel et al., 1994), as well as in all other known mytilids. As pointed out in Kenk & Wilson (1985: 260), the dorsal ends of the ascending lamellae are attached to muscular longitudinal ridges on the surfaces of the mantle lobes and the visceral mass. These muscular longitudinal ridges are also unique to B. thermophilus and were not evident in any other mussel examined for this report.

The hinge of B. thermophilus was originally described as edentulous (Kenk & Wilson, 1985). However, in specimens of B. thermophilus smaller than about 10 mm there are up to 25 "vertical striations" or denticles immediately posterior of the ligament and about 6 denticles located immediately below the umbones (Fig. 3–5). Other deep-sea mussel species described herein (Figs. 6–28) also have hinge denticulations as juveniles (Figs. 8–10, 18–20, 23, 25–27). These denticulations are lost in adult members of the genus Bathymodiolus

Although Bathymodiolus was described as lacking ventral food grooves on the ctenidia (Kenk & Wilson, 1985), we observed reduced food grooves in all specimens of B. thermophilus we examined. Food grooves were first described in B. thermophilus by Le Pennec et al. (1983), Le Pennec & Hily (1984), and Fiala-Médioni et al. (1986).

Kenk & Wilson (1985) described the periostracum of Bathymodiolus as "hirsute"; meaning hairy, bristly or shaggy. However, these "periostracal hairs" are probably of byssal origin (Bottjer & Carter, 1980; Ockelmann, 1983) and not of taxonomic value. The original description of Bathymodiolus described the labial palps as "small," whereas the labial palps of B. thermophilus specimens we examined, from the type-locality and elsewhere, were large and muscular.

Range: This species appears confined to the area of hydrothermal vent activity on the Galápagos Rift and along the EPR at 9° to 10°N, 11°24'N and 13°N (Table 2). In addition,
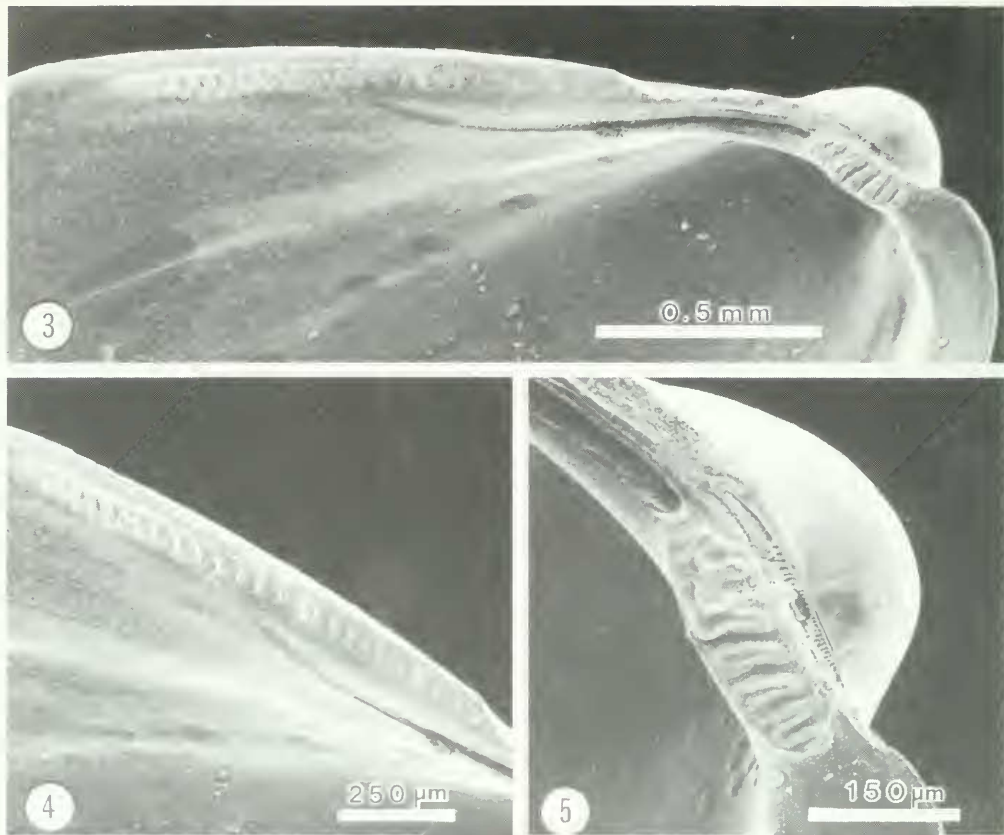
FIG. 3. Bathymodiolus thermophilus Kenk & Wilson. Juvenile hinge line of specimen 4.5 mm in length.
FIG. 4. Bathymodiolus thermophilus Kenk & Wilson. Hinge denticles, located immediately posterior to liga-ment in juvenile specimen 4.5 mm in length.
FIG. 5. Bathymodiolus thermophilus Kenk & Wilson. Hinge denticles, located immediately below the umbo in juvenile specimen 4.5 mm in length.

preliminary comparison of mtDNA COI se-quences between B. thermophilus from the type locality and mussels collected from 17°S on the EPR revealed essentially no differ-ences (R.C. Vrijenhoek, unpublished data).

Bathymodiolus heckerae Turner,
Gustafson, Lutz & Vrijenhoek, new species
Figures 6–13

This species, known since 1984, has been referred to in literature concerning seep and vent biology but was never formally de-scribed. The following is a list of these refer-ences.

"Mussel" — Paull et al., 1984: 965, fig. 2 [mus-sels visible in habitat photo].

"Mussels" — Florida Escarpment Cruise Par-ticipants, 1984: 32, fig. 1 [mussels visible in habitat photo].
"Large mussel" — Turner & Lutz, 1984: 60, figs. 1 (site #9 = Florida Escarpment, dia-gram of mussel shell), 5, 6, [mussels vis-ible in habitat photo], 8 (left) [micrograph of prodissoconch].
"Large, elongate mussels" — Turner, 1985: 29, figs. 4B–C, 6.
"Mytilid" — Southward, 1985: 673.
"Mytilid mussel" — Paull et al., 1985: 710.
"Large mussels," "large golden-brown my-tilids" — Hecker, 1985: 465, 466, figs. 2, 4, 5, 6 [mussels visible in habitat photos].
"Large mussels" — Grassle, 1986: 338.
"Seep mussels," "Florida Escarpment mus-sel" — Cavanaugh et al., 1987: 346, 347,

TABLE 2. Specimens of Bathymodiolus thermophilus examined.

Dive	Date	Depth	Latitude; Longitude	Number and condition of specimens
ALVIN Dives, Galápagos Rift				
887	12 Feb. 1979	2488	00°48.5'N; 86°09.1'W	1 - shell & tissue
983	30 Nov. 1979	2457	00°48.2'N; 86°13.4'W	2 - shell, 7 - shell & tissue
2223	28 May 1990	2503	00°47.9'N; 86°09.2'W	42 - shell
2224	29 May 1990	2461	00°48.2'N; 86°13.5'W	35 - shell
ALVIN Dives, East Pacific Rise 11°N				
2225	3 June 1990	2515	11°24.9'N; 103°47.3'W	15 - shell, 2 - shell & tissue
2226	4 June 1990	2515	11°24.9'N; 103°47.3'W	63 - shell
ALVIN Dives, East Pacific Rise 13°N				
2228	6 June 1990	2630	12°48.6'N; 103°56.5'W	14 - shell
2229	7 June 1990	2630	12°48.6'N; 103°56.5'W	51 - shell, 1 - shell & tissue
ALVIN Dives, East Pacific Rise near 9°N–10°N				
2350	31 March 1991	2585	09°30.9'N; 104°14.5'W	4 - shell
2351	1 April 1991	2550	09°50.1'N; 104°17.4'W	3 - shell
2352	2 April 1991	2567	09°33.5'N; 104°14.1'W	47 - shell
2354	4 April 1991	2527	09°47.7'N; 104°17.1'W	8 - shell
2356	6 April 1991	2556	09°40.9'N; 104°15.8'W	3 - shell
2358	8 April 1991	2578	09°30.9'N; 104°14.6'W	3 - shell & tissue
2359	9 April 1991	2564	09°30.9'N; 104°17.7'W	6 - shell
2368	19 April 1991	2539	09°51.1'N; 104°17.5'W	2 - shell
2498	6 March 1992	2525	09°50.5'N; 104°17.5'W	4 - shell & tissue

TABLE 3. Specimens of Bathymodiolus heckerae examined.

Dive	Date	Depth	Latitude; Longitude	Number and condition of specimens
ALVIN Dives, Gulf of Mexico - West Florida Escarpment				
1343	9 March 1984	3270	26°03'N; 84°54'W	14 - shell & tissue
1344	10 March 1984	3270	26°03'N; 84°56'W	1 - shell
1346	12 March 1984	3286	26°03'N; 84°54'W	1 - shell & tissue
1753	14 Oct. 1986	3277	26°02.4'N; 84°54.2'W	16 - shell
1754	15 Oct. 1986	3303	26°02.4'N; 84°55.3'W	4 - shell; 6, shell & tissue
1755	16 Oct. 1986	3300	26°01.5'N; 84°55.3'W	14 - shell, 2 - shell & tissue
1756	17 Oct. 1986	3243	26°01'N; 84°55'W	27 - shell
1758	20 Oct. 1986	3266	26°01.8'N; 84°54.9'W	4 - shell
2196	26 March 1990	3314	26°02.4'N; 84°54.4'W	91 - shell, 17 - shell & tissue
2197	29 March 1990	3314	26°02.2'N; 84°54.5'W	60 - shell
2542	3 June 1992	3313	26°01.8'N; 84°54.6'W	49 - shell, 40 -shell & tissue

TABLE 4. Specimens of Bathymodiolus brooksi examined.

Dive	Date	Depth	Latitude; Longitude	Number and condition of specimens
ALVIN Dives, Gulf of Mexico - Alamiños Canyon				
2209	11 April 1990	2340	26°21.1'N; 94°30.3'W	18 - shell
2211	13 April 1990	2222	26°21.3'N; 94°29.7'W	65 - shell, 20 - shell & tissue
2535	22 May 1992	2220	26°21.1'N; 94°29.5'W	6 - shell & tissue
ALVIN Dives, Gulf of Mexico - West Florida Escarpment				
1343	9 March 1984	3270	26°03'N; 84°54'W	1 - shell & tissue
2196	26 March 1990	3314	26°02.4'N; 84°54.4'W	1 - shell
2542	3 June 1992	3313	26 °01.8'N; 84°54.6'W	4 - shell, 3 -shell & tissue

TABLE 5. Specimens of "Bathymodiolus" childressi examined.

Dive	Date	Depth	Latitude; Longitude	Number and condition of specimens
JOHNSON SEA LINK-I Dives, Gulf of Mexico - Louisiana Continental Slope - Bush Hill				
1877	27 Sept. 1986	548	27°46.9'N; 91°30.4'W	5 - shell & tissue
3108	31 Aug. 1991	548	27°46.9'N; 91°30.4'W	3 - shell & tissue
3129	15 Sept. 1991	546	27°46.9'N; 91°30.4'W	119 - shell, 59 - shell & tissue
JOHNSON SEA LINK-I Dives, Gulf of Mexico - Louisiana Continental Slope - Green Canyon-272				
3133	17 Sept. 1991	737	27°41.3'N; 91°32.5'W	4 - shell
3137	19 Sept. 1991	723	27°41.1'N; 91°32.2'W	44 - shell, 8 -shell & tissue
JOHNSON SEA LINK-I Dives, Gulf of Mexico - Louisiana Continental Slope - Brine Pool NR-1				
3145	27 Sept. 1991	650	27°43.4'N; 91°16.6'W	29 - shell
ALVIN Dives, Gulf of Mexico - Alamiños Canyon				
2211	13 April 1990	2222	26°21.3'N; 94°29.7'W	31 - shell, 8 - shell & tissue

TABLE 6. Specimens of Tamu fisheri examined.

Dive	Date	Depth	Latitude; Longitude	Number and condition of specimens
JOHNSON SEA LINK-I Dives, Gulf of Mexico - Louisiana Continental Slope - Bush Hill				
3108	31 Aug. 1991	548	27°46.9'N; 91°30.4'W	6 - shell, 3 - shell & tissue
3129	15 Sept. 1991	546	27°46.9'N; 91°30.4'W	3 - shell & tissue
JOHNSON SEA LINK-I Dives, Gulf of Mexico - Louisiana Continental Slope - Near Garden Banks-386				
3131	16 Sept. 1991	701	27°50'N; 92°10'W	1 - single valve
3149	29 Sept. 1991	650	27°50'N; 92°10'W	6 - shell
MCZ No. 296151 (Texas A & M University, Louisiana Slope, Cruise #85-6-5, Trawl #5)				
L2787 (right valve)				
L2788 (left valve)				
L2789 (left valve)				
MCZ No. 296152 (Texas A & M University, Louisiana Slope, Cruise #85-6-5, Trawl #10)				
L2742 (right valve)				
L2743 (left valve)				
L2744 (left valve)				
L2745 (left valve)				

TABLE 7. Specimens of "Idas" macdonaldi examined.

Dive	Date	Depth	Latitude; Longitude	Number and condition of specimens
JOHNSON SEA LINK-I Dives, Gulf of Mexico - Louisiana Continental Slope				
3149	29 Sept. 1991	650	27°50'N; 92°10'W	4 - shell, 6 - shell & tissue

fig. 1a–b [micrographs of bacteriocyte and symbiotic bacterium].

"Mussels (c.f. Bathymodiolus)" – Hook & Golubic, 1988: 348, fig. 1 [mussels visible in habitat photos], fig. 2.

"Mytilid bivalve," "seep mussel" – Cary et al., 1989: 411.

"Deep-sea mussel, cf. Bathymodiolus" – Hook & Golubic, 1990: 240.

"Mytilid" – Petrecca & Grassle, 1990: 281.

"West Florida Escarpment mussel (common)" – Craddock et al., 1991: p. 302.

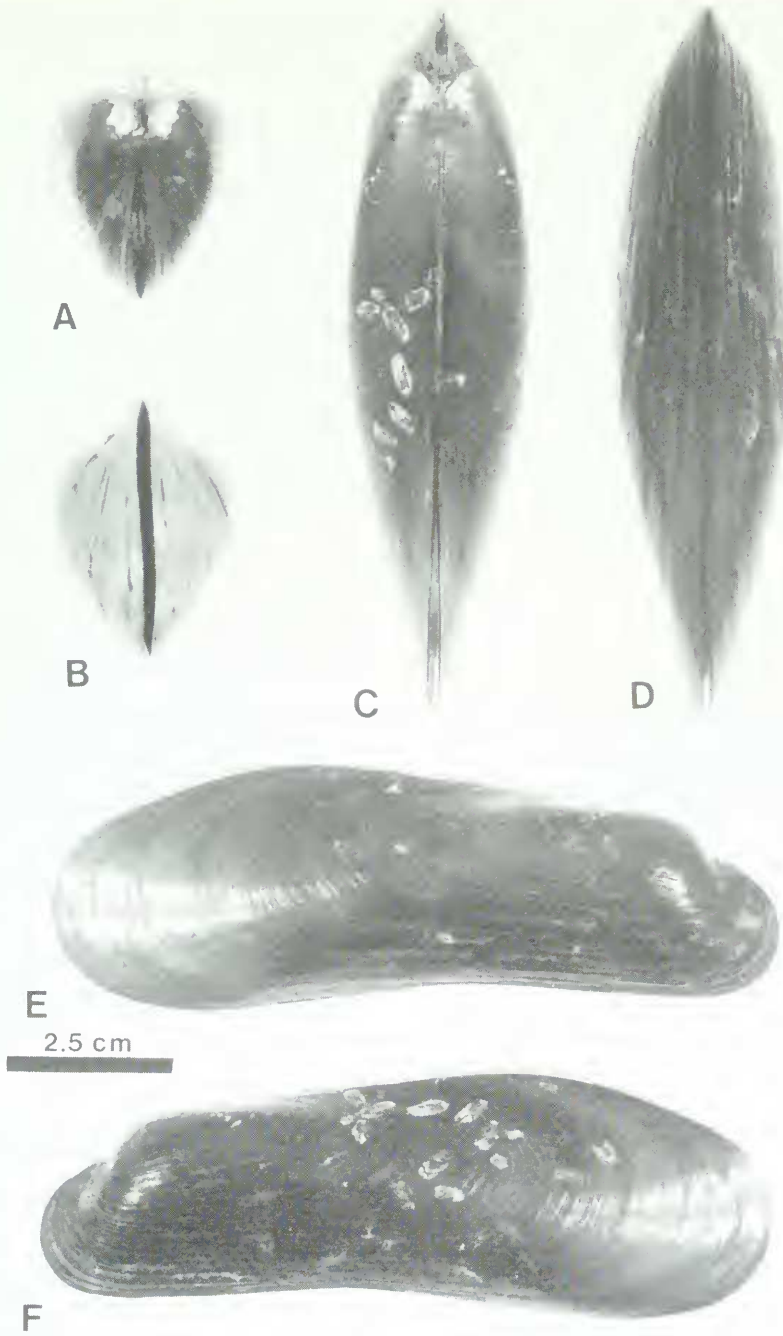"Florida Escarpment mussel" – Dahlhoff & Somero, 1991: 475 (table 1).

FIG. 6. Bathymodiolus heckerae Turner, Gustafson, Lutz & Vrijenhoek. Holotype, ANSP A18846. A, anterior view; B, posterior view; C, dorsal view; D, ventral view; E, lateral view of right valve; F, lateral view of left valve.

FIG. 7. Bathymodiolus heckerae Turner, Gustafson, Lutz & Vrijenhoek. External views of a growth series of shells illustrating ontogenetic change in shape.

"FL mytilid" – Cavanaugh, 1992: 316.
"Bathymodiolus-like mussels" – Hook & Golubic, 1992: 120.
"Seep mytilid Va" – Fisher, 1993: 609.
"Deep-sea mussel (an undescribed new genus similar to Bathymodiolus)" – Hook & Golubic, 1993: 81.
"SM Va" – Fisher et al., 1993: 278, 284.
"FL/Va" – Craddock, et al., 1995: 479–483.
"Seep Mytilid Va" – Nelson & Fisher, 1995: table 3.

Types: Holotype ANSP A18846 from ALVIN Dive 1343 along the base of the West Florida Escarpment in the eastern Gulf of Mexico at 26°03′N; 84°54′W, in 3270 m. Paratypes are from ALVIN Dive 1754 at 26°02.4′N; 84°55.3′W in 3303 m (USNM); ALVIN Dive 1755 at 26°01.5′N; 84°55.3′W in 3300 m (MCZ); ALVIN Dive 2196 at 26°02.4′N; 84°54.4′W in 3314 m (ANSP 400772;, USNM, HMNS, MNHN); ALVIN Dive 2197 at 26°02.2′N; 84°54.5′W in 3314 m (HMNS); and ALVIN Dive 2542 at 26°01.8′N; 84°54.6′W in 3314 m (ANSP 400771, 400773; MNHN).

Shell Morphology: Shell large, up to 190 mm long, modioliform, thin, fragile, essentially equivalve, elongately elliptical. Anterior margin sharply rounded; posterior margin broadly rounded; ventral margin straight in young specimens, with a slight ventral concavity in medium sized specimens, concavity more pronounced in larger specimens; dorsal margin broadly convex, more or less straight over span of the ligament (Figs. 6, 7, 11, 12). Umbones often eroded; prosogyrate; subterminal, positioned between 6% and 16% of the length of the shell from anterior end. An indistinct, raised, broadly rounded ridge extends from umbonal region to posterior-ventral margin.

External sculpture lacking; surface smooth except for concentric growth lines; fine radial lines in periostracum extending from umbo to ventral margin, most prominent posteriorly; and fine radial periostracal corrugations along the ventral margin in the region of the byssal gape. Shell dull-white, periostracum straw-yellow to light-brown in young specimens, older specimens have dark-brown perios-
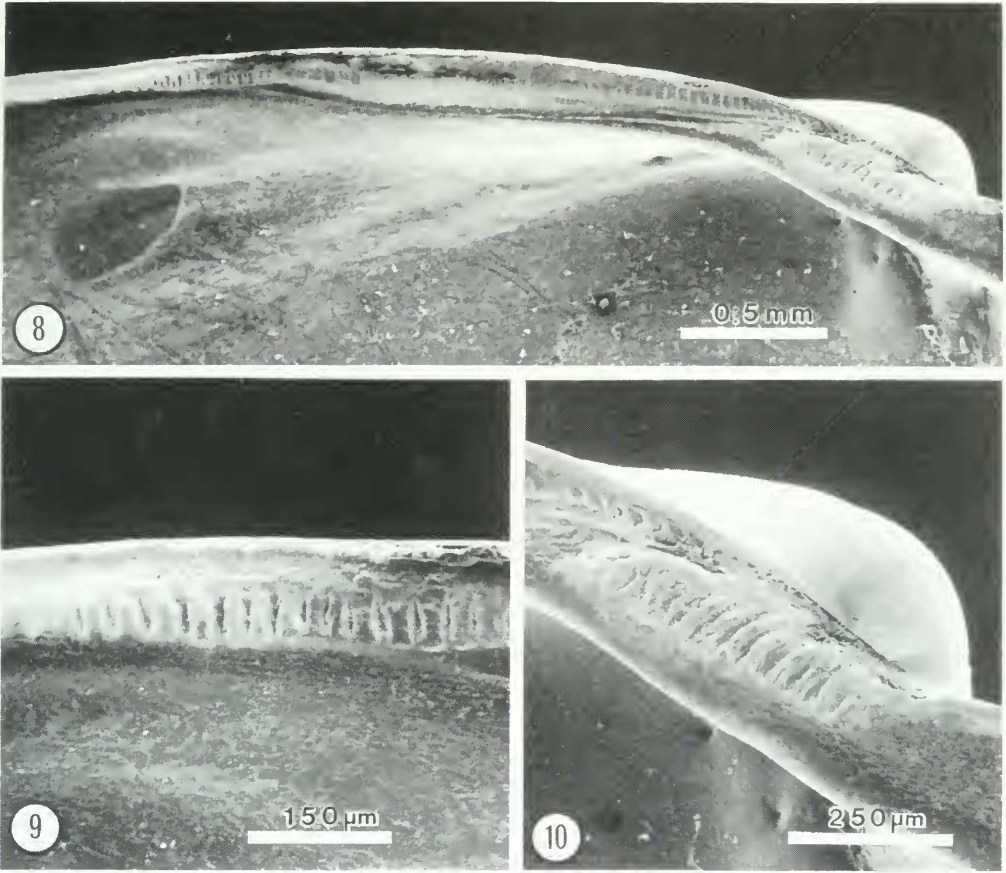
FIG. 8. Bathymodiolus heckerae Turner, Gustafson, Lutz & Vrijenhoek. Juvenile hinge line of specimen 7.5 mm in length.
FIG. 9. Bathymodiolus heckerae Turner, Gustafson, Lutz & Vrijenhoek. Hinge denticles located immediately posterior of the ligament in juvenile specimen 7.5 mm in length.
FIG. 10. Bathymodiolus heckerae Turner, Gustafson, Lutz & Vrijenhoek. Hinge denticles located immediately below the umbo in juvenile specimen 7.5 mm in length.

tracum that becomes straw-yellow peripherally. Periostracum of older specimens sometimes marked by irregularly shaped dark brown pigment patches, overlain by numerous byssal thread attachment plates. Interior off-white, predominately nacreous.

Ligament opisthodetic, parivincular, extending posteriorly from umbones to occupy from 32% to 49% of dorsal margin. Adult hinge edentulous, except for small posteriorly directed projection of anterior hinge margin beneath ligament's anterior end; hinge somewhat thickened below and anterior to umbo. Juvenile hinge with about 15 denticles imme-diately posterior to ligament and approximately 10 denticles located immediately below umbones (Figs. 8–10). Hinge denticles become obsolete in specimens greater than 18 mm in length.

Muscle Scars: Muscle scars and pallial line indistinct. Anterior adductor scar rounded but truncated posteriorly; located ventral and partially anterior to umbo in small specimens, entirely in front of umbo in medium and large specimens. Posterior adductor scar round to oblong, usually contiguous with small siphonal retractor scar ventrally and posterior portion of

posterior byssal-pedal retractor scar dorsally. Anterior retractor scar located within upper extremity of umbonal cavity directly beneath umbo. Posterior byssal retractors form two scars with very large intervening gap, anterior one obliquely elliptical, directly beneath or slightly anterior of posterior end of ligament in small specimens, well anterior of posterior end of ligament in medium and large specimens, second one elliptical, parallel to antero-posterior axis of shell and located antero-dorsally to and bordering posterior adductor scar (Fig. 12). Pallial line distant from shell margin, extending from postero-ventral edge of anterior adductor scar to postero-ventral edge of posterior adductor, curving slightly upwards and then downwards to form slight indentation in byssal gape region at about one-quarter to one-third of distance from anterior, end. Small siphonal retractor scar located at posterior end of ventral pallial line, usually but not always contiguous with posterior adductor (Fig. 12).

Selected Measurements (in mm):

length	height	width	anterior length	Dive	
110.6	36.0	28.1	—	A 1343	Holotype ANSP
75.2	27.8	22.3	9.7	A 1754	Paratype USNM
134.2	43.0	32.8	15.5	A 1755	Paratype MCZ
98.0	33.3	25.0	13.8	A 2196	Paratype HMNS
84.5	27.0	24.0	8.2	A 2196	Paratype MNHN
148.0	47.4	36.1	16.7	A 2196	Paratype Rutgers
22.6	11.4	7.8	1.8	A 2196	Paratype MNHN
38.7	17.5	13.8	3.2	A 2197	Paratype HMNS
102.0	34.0	25.5	11.5	A 2542	Paratype Rutgers
99.0	36.5	24.8	10.5	A 2542	Paratype ANSP
132.5	45.0	31.7	16.6	A 2542	Paratype ANSP
122.9	39.7	29.8	16.1	A 2196	Paratype ANSP
148.1	41.1	37.3	23.0	A 2196	Paratype HMNS
79.2	26.8	21.6	7.2	A 2196	Paratype USNM
164.0	47.0	41.7	18.4	A 2542	Paratype Rutgers

Internal Morphology

Musculature: Main features of musculature evident from previous description of muscle scars and illustrated in Figure 13. Posterior byssal retractors divided into two widely divergent main bundles that attach separately to shell, a posterior portion inserting along antero-dorsal edge of posterior adductor and an anterior portion inserting below and anterior to ligament's posterior end. Posterior portion of posterior byssal retractor long and slender resulting in an elongate and quite narrow region of shell attachment. Pedal retractors large and prominent, arising from dorso-lateral surface of foot mass and passing posteriorly along lateral aspect of anterior byssal retractors to become integrated with anterior and lateral region of anterior portion of posterior byssal retractors at point of shell attachment. Siphonal retractors integrated with pallial musculature, although there does appear to be a siphonal retractor scar on the shell. Anterior retractors long and slender, arising from dorso-lateral aspect of byssal-pedal mass and passing anteriorly to insert in antero-dorsal extremity of umbonal cavity. Pair of slender labial palp suspensors extend forward as branches of anterior retractors to attach to shell just behind and adjacent to anterior adductor. Posterior adductor rounded, anterior adductor rounded; one-half the size of posterior adductor.

Foot and Byssus: Foot long, thick; shape in preserved specimens variable, dependent on degree of contraction. Byssal strands gray to brown, wide, flat, unornamented. Byssal gland extending down foot behind byssal groove, without extension dorsal to origin of anterior retractors.

Mantle and Mantle Cavity: Connections between edge of ascending lamellae and surface of mantle lobes and visceral mass weak or lacking, resulting in incomplete separation of incurrent and excurrent chambers. Lacking muscular longitudinal ridges for attachment of ascending lamellae to mantle lobes and visceral mass (see Kenk & Wilson, 1985: 260). Ventral edges of inner mantle lobes not unusually thickened or muscular. Excurrent tubuliform siphon short, not capable of extension beyond perimeter of shell, lacking internal diaphragm in specimens examined. Horizontal branchial septum incomplete; fusion of inner mantle immediately below excurrent siphon forming short horizontal shelf, not directly attached to ventral edge of posterior adductor. Incurrent and excurrent chambers not completely separated posterior of posterior adductor; posterior end of gill axes attached
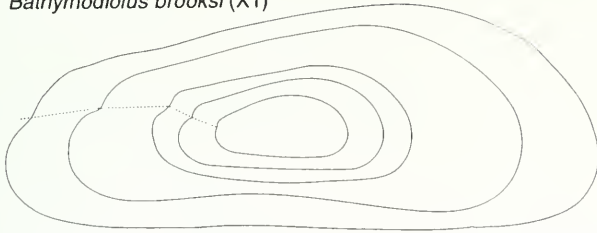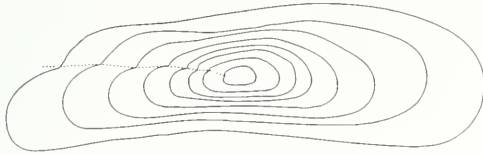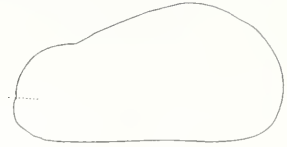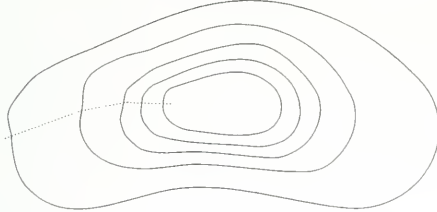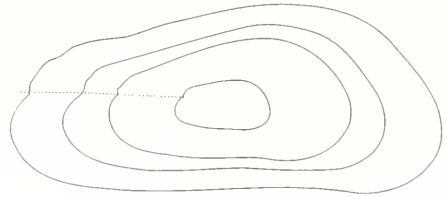
Bathymodiolus brooksi (X1)

50 mm

Bathymodiolus heckerae (X1)

"*Idas*" *macdonaldi* (X10)

"*Bathymodiolus*" *childressi* (X1)

Tamu fisheri (X2)

FIG. 11. Bathymodiolus heckerae, B. brooksi, "Bathymodiolus" childressi, Tamu fisheri, and "Idas" macdonaldi. Inset outlines of a graded series of shell outlines illustrating change in shape with increase in size. Only one specimen of "Idas" macdonaldi is illustrated. Dotted lines connect the relative positions of the anterior edge of the umbones in specimens of different size. Note scale bar and magnifications.

to ventral surface of horizontal branchial septum. Short extension as valvular siphonal membrane joins right and left mantle lobes, extending anteriorly only a short distance into pedal gape; small central papilla on anteriormost ventral extension of valvular siphonal membrane extends anteriorly into pedal gape. Pedo-byssal gape extensive; incurrent aperture extending from anterior end of valvular siphonal membrane to posterior edge of anterior adductor.

Ctenidia: Demibranchs thick, short; approximately equal-sized, both demibranchs extend anteriorly to same degree; ascending lamellae slightly shorter than descending. Ventral edges of demibranchs with poorly developed food grooves; dorsal food grooves present in deep folds just below junction of ascending lamellae and areas of attachment to mantle lobes and visceral mass. Filaments wide, fleshy; ctenidia and filaments light-brown. Distal interlamellar junctions lacking; descending and ascending portion of each filament con-

nected apically to one-quarter height of demibranch; every 2nd to 6th filament is "principal filament" [see Atkins, 1937: text fig. 18, type B(1b)] with septum rising to one-third height of demibranch. A single posterior "tubular connection" (see Kenk & Wilson, 1985) between free edges of ascending lamellae and gill axes sometimes present, indiscernible in some individuals.

Labial Palps: Paired labial palps greatly modified from typical filter-feeding type, appearing to function as sorting area for material gathered by foot rather than ctenidia. Base of inner and outer palp pair widely separated; ctenidia lie lateral of labial palps in preserved specimens. Mouth situated at basal mid-point of anterior end of inner pair of labial palps, farther posterior than typical for mytilids. Inner palp pair placed posteriorly, large and muscular, elongately triangular. Outer pair of palps more anterior, triangular, muscular, but smaller than inner pair. Oral groove on inner surface of both pair of palps, bordered by pli-
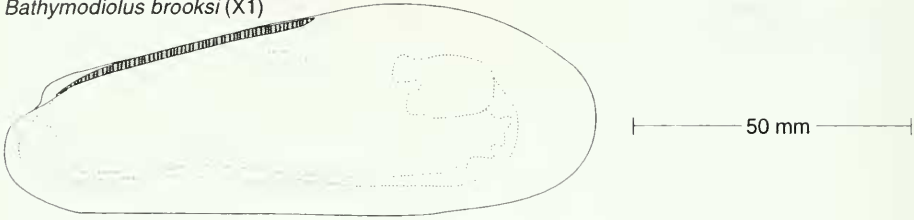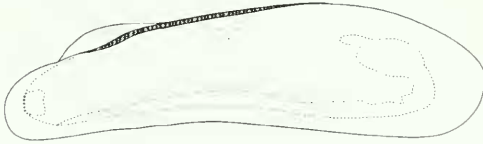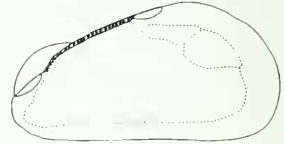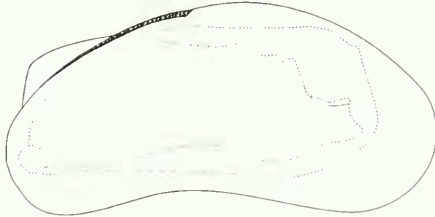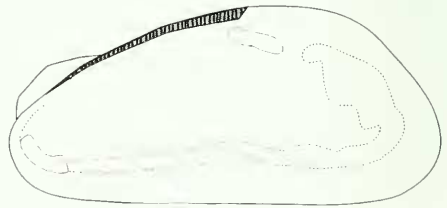
FIG. 12. Bathymodiolus heckerae, B. brooksi, "Bathymodiolus" childressi, Tamu fisheri, and "Idas" macdonaldi. Diagrams of left-lateral view of shell illustrating generalized location of muscle scars, pallial line and ligament. Lighter shading anterior and posterior to ligament in diagram of "Idas" macdonaldi indicates location of adult hinge denticles. Note scale bar and magnifications.

cations, running from near tip of proboscid-like extensions to mouth. Outer surfaces of palps smooth, non-plicate.

Digestive System: Alimentary tract straight with no recurrent loop, situated directly on body mid-line. Intestine leaves posterior end of stomach and traverses short distance posteriorly, merging with rectum; rectum enters extreme antero-ventral aspect of pericardium and ventricle, anterior to the level of the auricular openings into the ventricle.

Remarks: Bathymodiolus heckerae lacks both the extensive mid-ventral mantle fusion and the muscular longitudinal ridge in the mantle cavity, supporting the ascending lamellae, which are diagnostic characters of B. thermophilus. Bathymodiolus heckerae differs from B. brooksi in having a more arcuate shape, a greater relative shell length anterior to the umbo (A/L), larger and more prominent

pedal retractors, and a smaller height to length ratio at a given length (Fig. 28). It differs from "Bathymodiolus" childressi in having umbones more distant from the anterior, a less robust shell, widely separated posterior byssal retractors and associated scars, and a central papilla on the anterior rim of the valvular siphonal membrane.

Relationship with B. brevior, B. elongatus, and B. puteoserpentis (which were placed in this genus only provisionally) is difficult to assess since we know little about the internal anatomy of these species (Cosel et al., 1994), although the recently reported presence of two recurrent loops in the intestine of B. puteoserpentis (Cosel et al., 1997) distinguishes this species from B. heckerae and other mussels examined in this report. Bathymodiolus heckerae differs from these three species in being much more arcuate and elongated (Cosel et al., 1994). The shell shape of adult B. heckerae is also much more
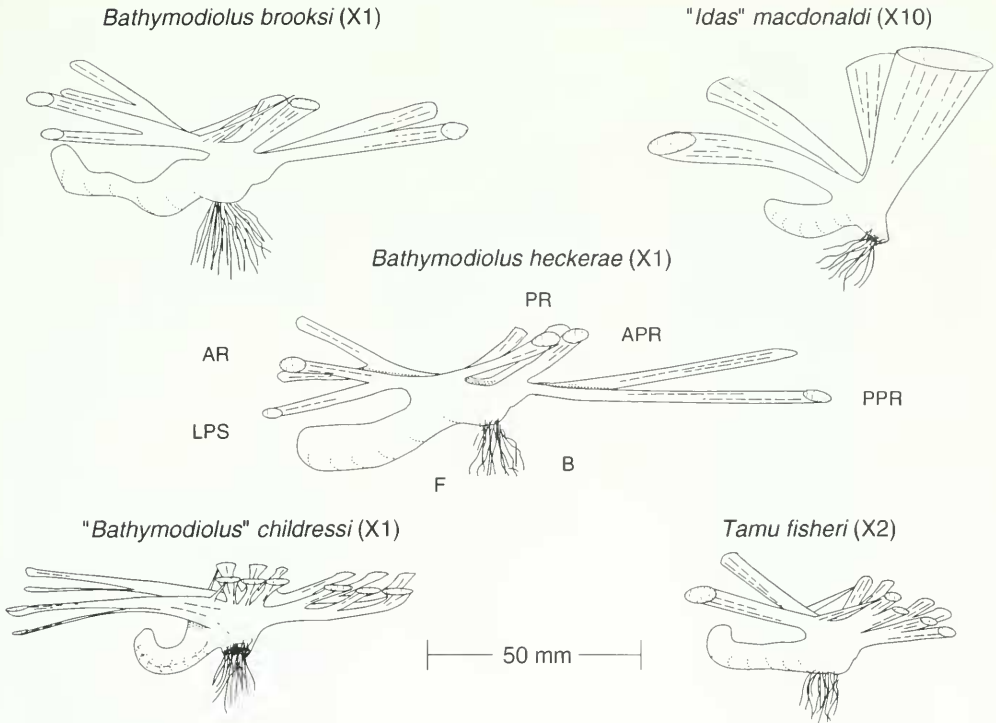
FIG. 13. Bathymodiolus heckerae, B. brooksi, "Bathymodiolus" childressi, Tamu fisheri, and "Idas" macdonaldi. Foot and retractor muscle masses as viewed from a left-lateral orientation. Anterior is to the left. Note scale bar and magnifications. AR, anterior byssal-pedal retractor; APR, anterior portion of posterior byssal retractor; B, byssus; F, foot; LPS, labial palp suspensor; PPR, posterior portion of posterior byssal retractor; PR, pedal retractor.

arcuate than any of the four Bathymodiolus species (platifrons, japonicus, aduloides, and septemdierum) from deep-sea sites off Japan. Bathymodiolus heckerae also differs from B. platifrons in having subterminal umbones (located between 6% and 16% of the anterior end of the shell) in comparison to the terminal umbones of B. platifrons (Hashimoto & Okutani, 1994).

In a protein electrophoretic study, Craddock et al. (1995) showed that B. heckerae (as FL/Va) and B. thermophilus (as MB/Bt) had no shared alleles at 17 of 26 gene loci and that these two species had a Nei's genetic distance (D) of 1.085 (Nei, 1978). Nei's genetic distance between B. heckerae, from the West Florida Escarpment site, and the two populations of B. brooksi from the West Florida Escarpment and Alamiños Canyon sites were 0.528 and 0.719, respectively. These genetic distances are within the range of values for

species-level separation. Bathymodiolus heckerae was more highly divergent in pairwise comparisons with "Bathymodiolus" childressi (D = 2.188 and 2.086 for Bush Hill and Alamiños Canyon samples), T. fisheri (D = 1.983), and "Idas" macdonaldi (D = 2.556) (Table 8; Craddock et al., 1995).

Analysis of a 246 bp region of the mtDNA COI gene showed a sequence divergence of 14.7% between B. heckerae and B. brooksi, and 17.6% to 18.7% between B. heckerae and "Bathmodiolus" childressi (Table 8; W. R. Hoeh, unpublished data). Percent sequence divergence between B. heckerae and T. fisheri was 52.2%, and 44.9% between B. heckerae and "Idas" macdonaldi (Table 8). These levels of allozymic and mtDNA divergence support separate species status for B. heckerae, as well as separation at the generic level from T. fisheri and "Idas" macdonaldi.

Two genetically (Cavanaugh, 1992; Ca-

TABLE 8. Genetic distance matrix. Nei's (1978) unbiased genetic distance (above diagonal) based on 26 allozyme loci (from Craddock et al., 1995). Percent sequence divergence (below diagonal) for 246 bp of mitochondrial COI (W. R. Hoeh, unpublished data). Site and Operational Taxonomic Unit (OTU) designations as in Craddock et al. (1995). Ia, Ib = "Bathymodiolus" childressi; II, Vb = Bathymodiolus brooksi; III = Tamu fisheri; IV = "Idas" macdonaldi; Va = B. heckerae; BH = Bush Hill, Louisiana Continental Slope; AC = Alamiños Canyon; GB = Garden Banks, Louisiana Continental Slope; FL = West Florida Escarpment.

Site/OTU	BH/Ia	AC/Ib	AC/II	GB/III	GB/IV	FL/Va	FL/Vb
BH/Ia	—	0.042	1.507	2.209	2.656	2.188	2.531
AC/Ib	0.83	—	1.531	2.138	2.570	2.086	2.434
AC/II	17.16	17.16	—	1.992	5.688	0.719	*
GB/III	48.74	47.91	50.28	—	1.859	1.983	2.552
GB/IV	44.95	43.37	41.85	37.97	—	2.556	3.258
FL/Va	17.63	18.73	14.73	52.22	44.95	—	0.528
FL/Vb	17.16	17.16	0.00	50.28	41.85	14.73	—

*Some minor allozyme differences may exist but they remain to be adequately resolved.

vanaugh et al., 1992) and morphologically distinct (Cavanaugh et al., 1987) bacteria are found within gill bacteriocytes of B. heckerae. One of these is a large coccus, about 1.6 μm in diameter, with stacked internal membranes typical of Type I methanotrophs and the other is a smaller coccus or rodshaped cell, about 0.4 μm in diameter, without internal membranes. Stable carbon isotope ratios, methanol dehydrogenase activity, and the presence of a gill symbiont with stacked internal membranes indicate that B. heckerae relies on its methanotrophic symbionts to some degree as a source of carbon and energy (Cavanaugh et al., 1987; Cary et al., 1989).

Many but not all specimens of B. heckerae harbor a commensal polynoid polychaete Branchipolynoe seepensis Pettibone, 1986, within the mantle cavity. A second polychaete, the nautiliniellid Laubierus mucronatus Blake, 1993, has also been described from the mantle cavity of B. heckerae (Blake, 1993). An additional nautiliniellid Flascarpia alvinae Blake, 1993, is present at the West Florida Escarpment site but its supposed bivalve host has not been determined (Blake, 1993).

An electrophoretic analysis of B. heckerae at this site (Craddock et al., 1991, 1995) revealed the presence of a single individual of a morphologically distinct congeneric mussel. Subsequently, eight additional specimens of this congener B. brooksi (described herein) were identified. Other faunal components of this site include the vestimentiferan Escarpia laminata Jones, 1985; the bresiliid shrimp Alvinocaris muricola Williams, 1988; the neolepetopsid limpet Paralepetopsis floridensis McLean, 1990; an undescribed vesicomyid bivalve, a coiled archaeogastropod, a large white turrid gastropod, serpulid polychaetes, galatheid crabs, anemones, holothurians, ophiuroids, and zoarcid fish (Paull et al., 1984; Hecker, 1985). Newly settled B. heckerae are often found attached by byssal threads within the eroded apices of the unnamed small coiled archaeogastropods which themselves are found crawling on the adult mussel shells at this site (Turner & Lutz, 1984; Turner, 1985). The small prodissoconch I and large prodissoconch II of B. heckerae suggests a planktotrophic mode of larval development (Turner & Lutz, 1984).

Etymology: The specific name honors Dr. Barbara Hecker who was among the first scientists to describe the cold-water seep fauna of the West Florida Escarpment. The working designation "Seep Mytilid Va" was given to this species.

Range: Known only from cold-water methane/sulfide seeps at the base of the West Florida Escarpment in the eastern Gulf of Mexico near 26°02′N and 84°55′W, in depths from 3243 to 3314 m (Table 3).

Bathymodiolus brooksi Gustafson, Turner, Lutz & Vrijenhoek, new species
Figures 11–15

This species, known since 1990, has been referred to in literature concerning seep and vent biology but was never formally described. The following is a list of these references.

"Mussels" (in part) — Brooks et al., 1990: 1772.
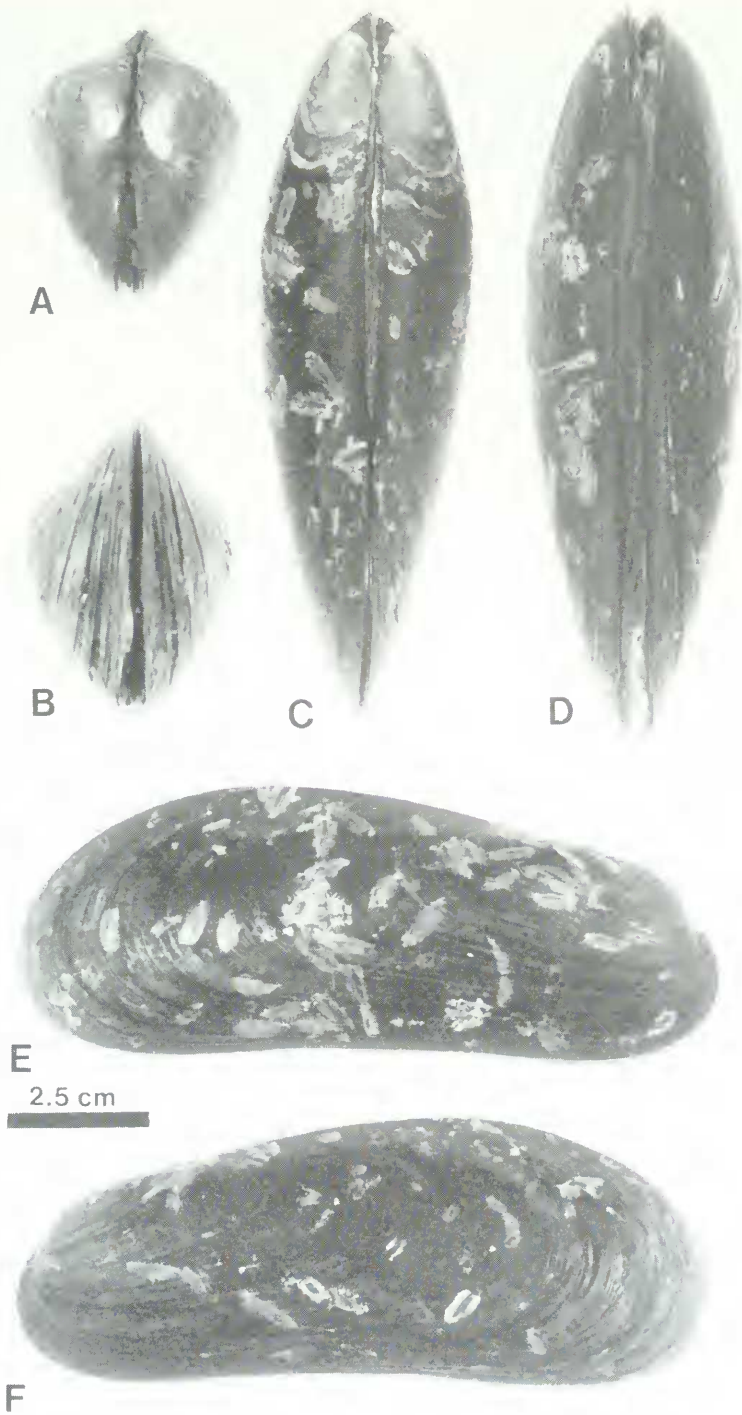
FIG. 14. Bathymodiolus brooksi Gustafson, Turner, Lutz & Vrijenhoek. Holotype, ANSP A18847. A, anterior view; B, posterior view; C, dorsal view; D, ventral view; E, lateral view of right valve; F, lateral view of left valve.
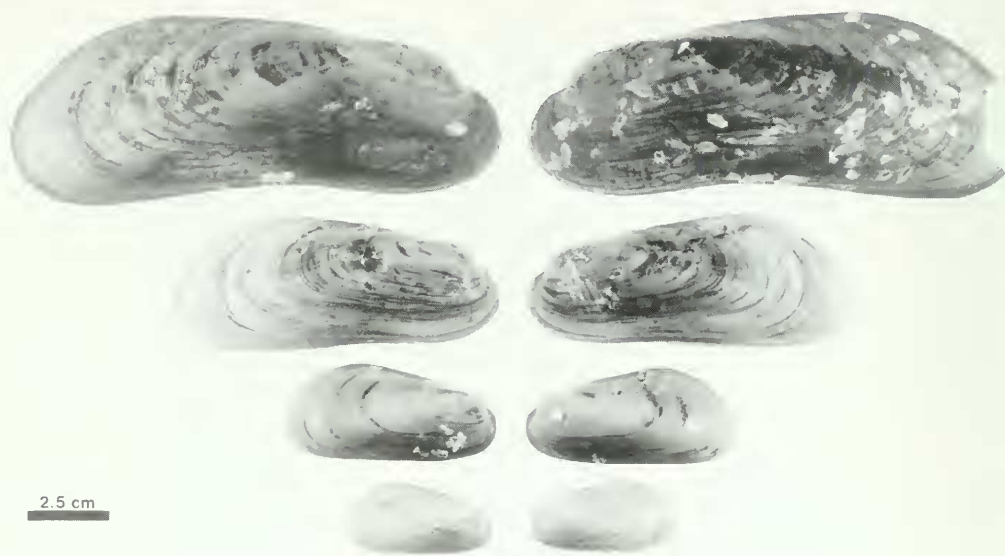
FIG. 15. Bathymodiolus brooksi Gustafson, Turner, Lutz & Vrijenhoek. External views of a growth series of shells illustrating ontogenetic change in shape.

"Alaminos Canyon more common mussel" – Craddock et al., 1991: 302.

"West Florida Escarpment mussel (one individual)" – Craddock et al., 1991: 302.

"Alaminos Canyon sp. A" - Fisher et al., 1991: 134A.

"Seep mytilid II," "Seep mytilid Vb" – Fisher, 1993: 609.

"Seep Mytilid II," "SM II" – Fisher et al., 1993: 278, 280–287, fig. 1 [mussels in habitat photo], figs. 2, 3 [micrographs of symbiotic bacteria in gills].

"AC/II, FL/Vb" – Craddock, et al., 1995: 479–483.

"Seep Mytilid II" – Nelson & Fisher, 1995: 134, table 3.

Types: Holotype ANSP A18847 from ALVIN Dive 2211 in the western Gulf of Mexico at a hydrocarbon seep in Alamiños Canyon at 26°21.3'N; 94°29.7'W in 2222 m. A number of paratypes (ANSP 400775, USNM, MCZ, HMNS, MNHN) are from the same dive and locality. Additional paratypes are from ALVIN Dive 2209 in Alamiños Canyon at 26°21.1'N; 94°30.3'W in 2340 m (ANSP 400774, USNM, MCZ, HMNS) and from the base of the West Florida Escarpment in the eastern Gulf of Mexico from ALVIN Dive 2196 at 26°02.4'N; 84°54.4'W in 3314 m (ANSP 400777), and

ALVIN Dive 2542 at 26°01.8'N; 84°54.6'W in 3313 m (ANSP 400776, USNM, HMNS).

Shell Morphology: Shell large, up to 180 mm long, modioliform, elongate, elliptical, thin and fragile, essentially equivalve. Anterior margin moderately rounded; posterior margin broadly rounded; ventral margin straight in young specimens, with slight ventral concavity in medium sized specimens, concavity more pronounced in larger specimens; dorsal margin very broadly convex, more or less straight over span of the ligament (Figs. 11, 12, 14, 15). Umbones of largest specimens eroded; prosogyrate; subterminal, positioned within anterior one-tenth. An indistinct, raised, broadly rounded ridge extends from umbonal region to posterior-ventral margin.

External surface sculpture lacking, smooth except for concentric growth lines, fine radial lines in periostracum extending from umbo to ventral margin, and fine radial periostracal corrugations in the median ventral area. Shell dull-white beneath dark-brown to straw-yellow periostracum. Periostracum often marked by irregularly shaped dark brown pigment patches, overlain by numerous byssal thread attachment plates. Interior off-white, predominately nacreous.

Ligament opisthodetic, parivincular, ex-

tending posteriorly from umbones to occupy from 41% to 59% of dorsal margin. Adult hinge edentulous, except for posteriorly directed projection of anterior hinge margin beneath anterior end of ligament, hinge thickened below and anterior to umbo. Hinge denticles absent in smallest specimen (36 mm length) observed.

Muscle Scars: Anterior adductor scar rounded but truncated posteriorly, located below and partially anterior to umbo, distant from antero-ventral margin. Posterior adductor scar round, contiguous with small siphonal retractor scar ventrally and posterior portion of posterior byssal retractor scar dorsally. Anterior retractor scar located in posterior portion of umbonal cavity. Posterior byssal retractors form two scars with large intervening gap; anterior one elliptical, directly beneath or slightly anterior of posterior end of ligament; second one elliptical, parallel to antero-posterior axis of shell and located antero-dorsally to and bordering posterior adductor scar (Fig. 12). Pallial line distant from shell margin, extending from postero-ventral edge of anterior adductor scar to posterior adductor, curving slightly upwards and then more strongly downwards to form an indentation in byssal gape region at about one-quarter to one-third of distance from anterior; small siphonal retractor scar located at posterior end of ventral pallial line, usually but not always contiguous with posterior adductor.

Measurements (in mm):

length	height	width	anterior length	Dive	
121.3	46.8	35.4	—	A 2211	Holotype ANSP
152.0	60.3	45.8	12.6	A 2211	Paratype MCZ
142.2	54.4	39.7	11.3	A 2211	Paratype USNM
125.9	48.6	44.5	9.0	A 2211	Paratype MNHN
40.0	20.3	13.0	2.7	A 2211	Paratype ANSP
171.0	64.9	49.0	10.5	A 2209	Paratype MCZ
132.7	48.4	36.0	12.7	A 2209	Paratype MCZ
116.4	44.6	30.5	9.3	A 2209	Paratype MCZ
141.4	51.0	38.9	11.3	A 2209	Paratype ANSP
166.0	61.8	44.0	14.4	A 2209	Paratype Rutgers
132.3	54.4	40.3	9.4	A 2211	Paratype MNHN
146.0	49.5	42.0	12.5	A 2209	Paratype Rutgers
143.4	55.5	42.0	13.0	A 2209	Paratype HMNS
106.3	42.2	34.7	8.8	A 2211	Paratype Rutgers
85.5	35.7	24.6	5.0	A 2196	Paratype ANSP
127.7	55.4	40.1	9.0	A 2542	Paratype USNM
117.5	42.4	30.0	6.0	A 2542	Paratype HMNS
88.2	36.7	28.6	5.2	A 2542	Paratype ANSP

Internal Morphology

Musculature: Main features of musculature evident from previous description of muscle scars and Figure 13. Posterior byssal retractors divided into two widely divergent main bundles that attach separately to shell, a posterior portion inserting along postero-dorsal edge of posterior adductor and an anterior portion attaching to shell just below ligament's posterior end. Posterior pedal retractors very thin, arising from antero-dorsal part of foot, passing lateral to anterior retractors and inserting on shell anterior and lateral to posterior portion of posterior byssal retractors. Siphonal retractors integrated with pallial musculature. Anterior retractors arising from dorso-lateral section of byssal-pedal mass and passing anteriorly to insert in antero-dorsal extremity of umbonal cavity. Pair of slender labial palp suspensors extend forward as branches of anterior retractors to attach to shell just behind and adjacent to anterior adductor. Posterior adductor oblong; anterior adductor round in cross-section, about one-half size of posterior adductor.

Foot and Byssus: Foot long, thick; shape in preserved specimens variable, dependent on degree of contraction. Byssal strands light to dark brown, wide, flat, unornamented. Byssal gland extending down foot behind byssal groove, without extension dorsal to origin of anterior byssal retractors.

Mantle and Mantle Cavity: Connections between edge of ascending lamellae and surface of mantle lobes and visceral mass weak or lacking, resulting in incomplete separation of incurrent and excurrent chambers. Lacking muscular longitudinal ridges for attachment of ascending lamellae to mantle lobes and visceral mass (see Kenk & Wilson, 1985: 260).

Ventral edges of inner mantle lobes thickened, muscular. Excurrent tubuliform siphon capable of slight extension beyond perimeter of shell, lacking internal diaphragm in specimens examined. Horizontal branchial septum incomplete; fusion of inner mantle immediately below excurrent siphon forms short horizontal shelf, not directly attached to ventral edge of posterior adductor. Incurrent and excurrent chambers not completely separated posterior of posterior adductor; posterior end of gill axes attach to ventral surface of horizontal branchial septum. Short extension as valvular siphonal membrane joins right and left mantle lobes, extending anteriorly a short distance into pedal gape; small central papilla on valvular siphonal membrane extending anteriorly into pedal gape. Pedo-byssal gape extensive; incurrent aperture extending from anterior end of valvular siphonal membrane to posterior edge of anterior adductor.

Ctenidia: Demibranchs approximately equal-sized, thick, short; ventral edges with poorly developed food grooves; dorsal food grooves present in deep folds just below junction of ascending lamellae and areas of attachment to mantle lobes and visceral mass. Filaments wide, fleshy; ctenidia and filaments light-brown. Distal interlamellar junctions lacking; descending and ascending portion of each filament connected apically to one-quarter height of demibranch; every 2nd to 5th filament is "principal filament" (see Atkins, 1937: text fig. 18, type B [1b]) with septum rising to greater than one-third height of demibranch. Lacking "tubular connections" (see Kenk & Wilson, 1985) between free edges of ascending lamellae and gill axes.

Labial Palps: Paired labial palps broadly triangular, thick, muscular; inner pair more posterior than outer pair, but not markedly so; plicate ventral to oral groove on inner surface of inner palp and dorsal to oral groove on inner surface of outer palp; outer palp surfaces smooth. Mouth situated in normal anterior position at basal junction of inner and outer palps. Antero-ventral portion of demibranchs situated between inner and outer palps coincident with plicate palp surfaces.

Digestive System: Alimentary tract essentially straight, without recurrent loop, situated directly on body mia-line. Intestine leaves posterior end of stomach and traverses posteriorly ventral to pericardium to a level just

posterior to ventricle's mid-point; rectum enters pericardium and ventricle from below at mid-point of ventricle, but anterior to level of auricular openings.

Remarks: Although specimens of B. brooksi from the West Florida Escarpment were more variable in shell shape than those from Alamiños Canyon, overall morphological differences between these were minor. Craddock et al. (1995) identified a single unique individual (with the OTU label FL/Vb; B. brooksi) among 94 specimens of FL/Va (B. heckerae) from this site. Once aware of the existence of a genotypically unique individual in this collection, visual examination of the voucher shell collection readily identified the lone individual. Although this one specimen appeared to differ genetically from all other deep-sea mussels examined by Craddock et al. (1995), analysis of additional specimens of FL/Vb (B. brooksi) collected from this site in 1993 showed that these new FL/Vb samples did not differ from AC/II (B. brooksi from Alamiños Canyon), indicating that B. brooksi is present both at Alamiños Canyon and the West Florida Escarpment sites (Table 8). In addition, analysis of mt DNA COI sequences revealed that the new FL/Vb specimens from West Florida Escarpment were identical with B. brooksi from Alamiños Canyon (AC/II) (Table 8; W. R. Hoeh, unpublished data).

Bathymodiolus brooksi lacks both the extensive ventral mantle fusion and the muscular longitudinal ridge in the mantle cavity, supporting the ascending lamellae, that are characteristic of B. thermophilus. Bathymodiolus brooksi differs from B. heckerae in having a more anteriorly located umbo, a less arcuate ventral shell margin, and relatively thin pedal retractors. In addition, the height to length ratio of B. brooksi is normally greater than B. heckerae at a given length (Fig. 28). Bathymodiolus brooksi differs from "Bathymodiolus" childressi in having widely separated anterior and posterior portions of the posterior byssal retractors, whereas posterior byssal retractors are separated into multiple bundles with a single muscle scar in "Bathymodiolus" childressi. Bathymodiolus brooksi has a central papilla on the anterior margin of the valvular siphonal membrane, which is missing in "Bathymodiolus" childressi. In B. brooksi, the intestine is straight and the rectum enters the ventricle anterior to the auricular ostia; whereas in "Bathymodiolus" childressi, the intestine has a very short recurrent

loop and the rectum enters the ventricle posterior to the auricular ostia. In addition, B. brooksi differs from "Bathymodiolus" childressi in having a more elongate, more slender and less tumid shell shape.

Bathymodiolus brooksi differs from B. platifrons in having subterminal umbones (within 3% to 10% of the anterior) in comparison to the terminal position of the umbo in B. platifrons. The relative height of the posterior portion of the shell is much less in B. brooksi (H/L ranges from 0.34 to 0.51) than in B. platifrons (H/L range; 0.50 to 0.68) and B. japonicus (H/L range; 0.51 to 0.61). Bathymodiolus brooksi differs from B. aduloides in having a straight, unlooped intestine and a central papilla on the valvular siphonal membrane. A central papilla on the valvular siphonal membrane is also lacking in B. septemdierum (Hashimoto & Okutani, 1994).

Relationship between B. brooksi and B. brevior, B. elongatus, and B. puteoserpentis is difficult to assess since we know little about the internal anatomy of the latter three species (Cosel et al., 1994), although the recently reported presence of two recurrent loops in the intestine of B. puteoserpentis (Cosel et al., 1997) distinguishes this species from B. brooksi and other mussels examined in this report. Bathymodiolus brevior, B. elongatus, and B. puteoserpentis are much wider relative to their length than is B. brooksi; the ratio of width over length for B. brooksi ranges from 0.25 to 0.35, whereas these ratios in B. brevior, B. elongatus, and B. puteoserpentis are greater than 0.35.

The protein electrophoretic study of Craddock et al. (1995) showed that B. brooksi from Alamiños Canyon (designated as AC/II) and B. thermophilus (designated as MB/Bt) had no shared alleles at 17 of 26 gene loci and that these two species had a Nei's genetic distance (D) of 1.280. Nei's genetic distance between B. brooksi from Alamiños Canyon and B. heckerae from the West Florida Escarpment site was 0.719 (Craddock et al., 1995; see Table 8). These genetic distances are within the range of values for species-level separation. Bathymodiolus brooksi was more highly divergent in pairwise comparisons with "Bathymodiolus" childressi (D = 1.507 and 1.531 for Bush Hill and Alamiños Canyon samples), T. fisheri (D = 1.992), and "Idas" macdonaldi (D = 5.688) (Table 8; Craddock et al., 1995). Bathymodiolus brooksi shared only 8 to 9 of 26 alleles with "Bathymodiolus" childressi, only 4 of 26 alleles with T. fisheri, and

only 1 of 26 with "Idas" macdonaldi (Craddock et al., 1995). Since most congeneric groupings of animals have Nei's D values less than 2.0 (Nei, 1987), these results support generic separation of T. fisheri and "Idas" macdonaldi from B. brooksi.

Analysis of a 246 bp region of the mtDNA COI gene showed a sequence divergence of 14.7% between B. brooksi and B. heckerae, and 17.1% between B. brooksi and " Bathymodiolus" childressi (Table 8; W. R. Hoeh, unpublished data). Percent sequence divergence between B. brooksi and T. fisheri was 50.3%, and 41.8% between B. brooksi and "Idas" macdonaldi (Table 8). These levels of allozymic and mtDNA divergence support separate species status for B. brooksi, as well as separation at the generic level from T. fisheri and "Idas" macdonaldi.

General features of the Alamiños Canyon hydrocarbon/brine seep sites are presented in Brooks et al. (1990). Simultaneous occurrence of sulfur-oxidizing and methanotrophic bacterial symbionts in gill tissue, as well as the presence of two morphological types of symbionts visible in transmission electron micrographs of the gill tissue, suggests that B. brooksi harbors both thiotrophic and methanotrophic bacterial symbionts within its gill bacteriocytes (Fisher et al., 1993). Specimens of this species from the West Florida Escarpment site also harbor two morphologically distinct bacterial endosymbionts (C. M. Cavanaugh, pers. comm.).

Bathymodiolus brooksi shares the Alamiños Canyon site with the methanotrophic mussel "Bathymodiolus" childressi, two species of vestimentiferan tubeworms, a white shrimp, and galatheid crabs (Brooks et al., 1990). This species shares the West Florida Escarpment site with B. heckerae. Other West Florida Escarpment site fauna are described in the remarks section for B. heckerae.

Etymology: The specific name honors Dr. James M. Brooks, Texas A & M University, who has been one of the driving forces behind exploration of deep-sea hydrocarbon/brine seeps in the Gulf of Mexico. The working designation "Seep Mytilid II" was given to this species from Alamiños Canyon and "Seep Mytilid Vb" to members of this species from the West Florida Escarpment.

Range: Known from hydrocarbon seeps at Alamiños Canyon in the western Gulf of Mexico in depths from 2222 to 2340 m and from

cold-water methane/sulfide seeps at the base of the West Florida Escarpment in the eastern Gulf of Mexico near 26°02′N; 84°55′W in depths from 3270 to 3314 m (Table 4).

"Bathymodiolus" childressi Gustafson, Turner, Lutz & Vrijenhoek, new species
Figures 11–13, 16–20

This species, known since 1985, has been referred to in literature concerning seep and vent ecology but was never formally described. The following is a list of these references.

"Mytilid (large, brown)" – Turner, 1985: 29 (Louisiana Slope).
"Undescribed mussel" – Childress et al., 1986: 1306, fig. 2 [micrographs of gill filament and symbiotic bacteria].
"Mytilid" – Grassle, 1986: 339.
"Undescribed mytilid" – Fisher et al., 1986: 6A.
"Mussels" – Brooks et al., 1987a: 498.
"Mussels," "Mytilidae undescribed" – Brooks et al., 1987b: 1138, 1139.
"Seep mussels," "symbiont-containing mytilid bivalve" – Cary et al., 1988: 78, 79.
"Undescribed hydrocarbon-seep mussels" – Fisher et al., 1987: 59, figs. 1a, 1b, 2a, 3a, 3c [micrographs of gill filaments, bacteriocytes, symbiotic bacteria].
"Mussels from Louisiana hydrocarbon seeps" – Hook & Golubic, 1988: 361–362.
"Mussel" – Kennicutt et al., 1988a: 44, figs. 1, 2 [mussels visible in habitat photos].
"Mussel" – Kennicutt et al., 1988b: 1639.
"Undescribed seep mussel" – Page et al., 1988: 192A.
"Undescribed mussel (Mytilidae)" – Brooks et al., 1989:2.
"Methane-oxidizing mussel," "Bathymodiolus-like," "seep mussels" – MacDonald et al., 1989: 235, figs. 3C and 3D [mussels visible in habitat photos].
"Mussels," "Mytilidae sp." – Wade et al., 1989: 19, 22.
"Bathymodiolus n. sp." – MacDonald et al., 1990a: 1096, figs. 3, 4 [mussels visible in habitat photos].
"Seep mussel (Bathymodiolus n. sp.: Mytilidae)" – MacDonald et al., 1990b: 248, fig. 4 [mussels visible in habitat photos].
"Methanotrophic mussels" – MacDonald et al., 1990c: 15, figs. 2a–c [mussels visible in habitat photos].
"Mussels" – Alper, 1990a: 536, fig. p. 537 [mussels visible in habitat photo].

"Mussels" – Alper, 1990b: 23, figs. pp. 22, 26, 28 [mussels visible in habitat photos].
"Undescribed seep mussel" – Page et al., 1990: 251.
"Louisiana seep mussel" – Dahlhoff & Somero, 1991: 475 (table 1).
"Bathymodiolus sp." – Warén & Ponder, 1991: 54.
"Alaminos Canyon less common mussel" – Craddock et al., 1991: 302.
"Alaminos Canyon sp. B" – Fisher et al., 1991: 134A.
"Bathymodiolus sp., undescribed" – Kochevar et al., 1992: 389, fig. 4 [micrographs of gill filament and symbiotic bacteria].
"Bathymodiolus sp., undescribed" – Lee et al., 1992: 99.
"Louisiana seep mussel" – Kennicutt et al., 1992: 298.
"Seep Mytilid Ia" – Fisher & Childress, 1992: 223, fig. 2 [micrographs of bacteriocytes, symbiotic bacteria].
"LA mytilid" – Cavanaugh, 1992: 316.
"Seep mytilid Ia," "Seep mytilid Ib" – Fisher, 1993: 609.
"SM Ia, SM Ib" – Fisher et al., 1993: 278, 280.
"Seep Mytilid Ia" – Gustafson & Lutz, 1994: 80, figs. 4.1, 4.2 [micrographs of prodissoconch I and II].
"BH/Ia, AC/Ib" – Craddock et al., 1995: 479–483.
"Seep Mytilid Ia," "Seep Mytilid Ib" – Nelson & Fisher, 1995: 133–134, table 3.
"Seep mytilid Ia" – Lee & Childress, 1995: 137.
"Seep Mytilid Ia" – Nix et al., 1995: 605, 606, 609–613.
"Seep mytilid Ia" – Lee & Childress, 1996: 373.
"Seep Mytilid Ia" – Kochevar & Childress, 1996: tables 1, 2.

Types: Holotype ANSP A18848 from JOHNSON SEA-LINK-I Dive 3129, Bush Hill hydrocarbon seep, 27°46.9′N; 91°30.4′W, about 210 km south southwest of Grand Isle, Louisiana in 546 m. The type-locality is on the Louisiana Continental Slope between Blocks 184 and 185 in the Green Canyon offshore petroleum leasing area. Several paratypes (ANSP 400778, MCZ, HMNS, MNHN) are from the same locality. Additional paratypes are from JOHNSON SEA LINK-I Dive 3137 at 27°41.1′N; 91°32.2′W in 723 m (Green Canyon-272) (MCZ, HMNS, MNHN); JOHNSON SEA LINK-I Dive 3145 at 27°43.4′N; 91°16.6′W in 650 m (Brine Pool NR-1)
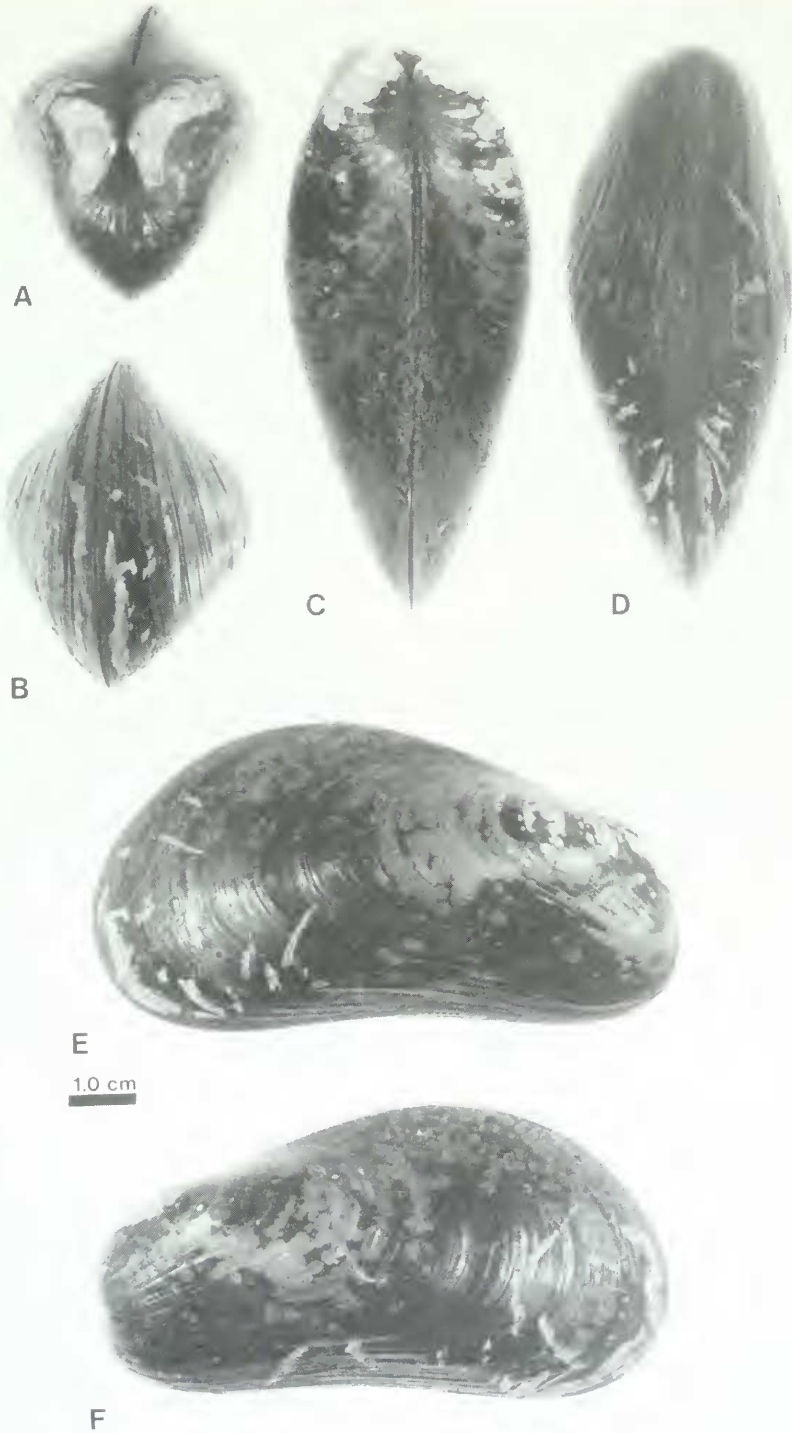
FIG. 16. "Bathymodiolus" childressi Gustafson, Turner, Lutz & Vrijenhoek. Holotype, ANSP A18848. A, anterior view; B, posterior view; C, dorsal view; D, ventral view; E, lateral view of right valve; F, lateral view of left valve.
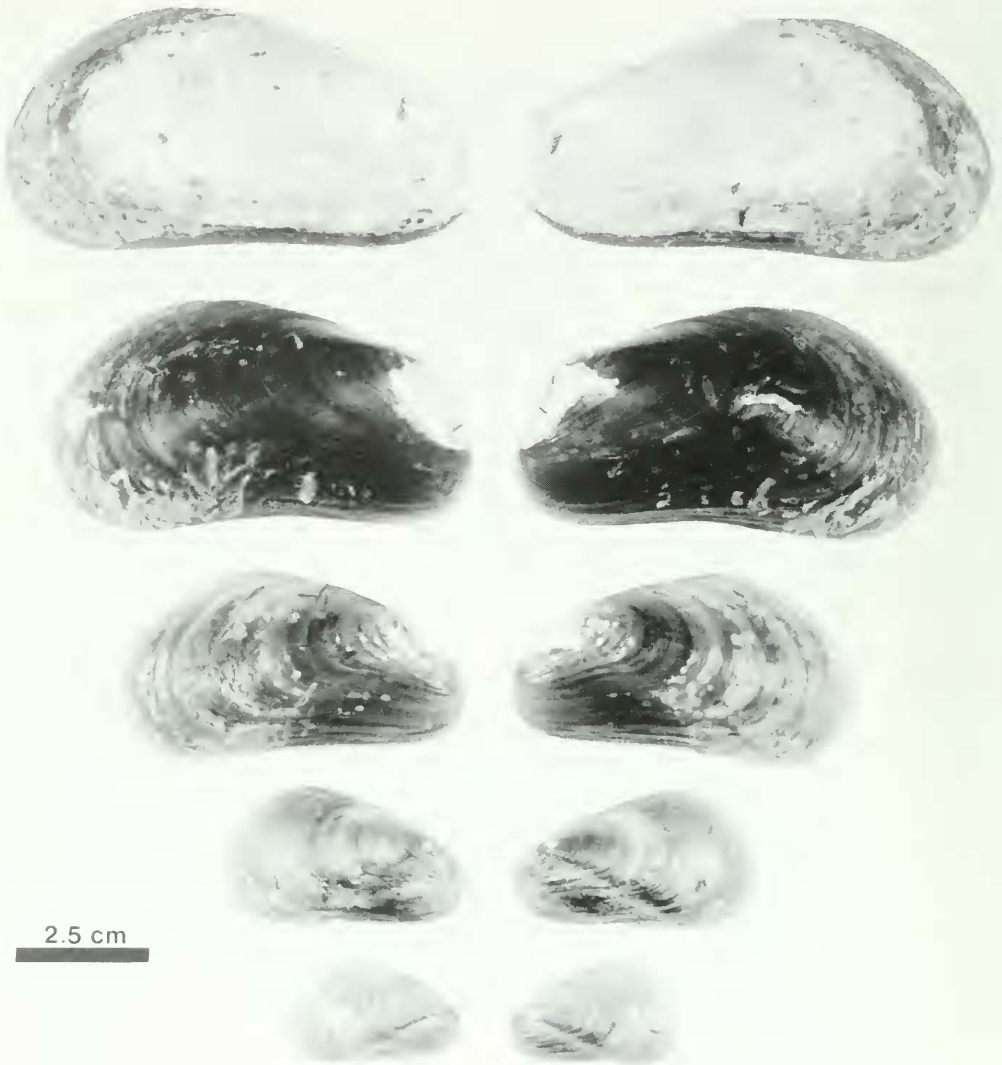
2.5 cm

FIG. 17. "Bathymodiolus" childressi Gustafson, Turner, Lutz & Vrijenhoek. External views of a growth series of shells illustrating ontogenetic change in shape.

(USNM, MCZ); and ALVIN Dive 2211 at 26°21.3'N; 94°29.7'W in 2222 m (Alamiños Canyon) (ANSP 400779, USNM, HMNS, MNHN).

Shell Morphology: Shell large, up to 120 mm long, modioliform, thin and fragile, essentially equivalve, elliptical in immature specimens, becoming increasingly arcuate in larger, old specimens (Figs. 11, 12, 16, 17). Anterior margin narrowly rounded; posterior margin broadly rounded; ventral margin straight to slightly concave in small specimens, becoming increasingly concave in larger specimens; dorsal margin convex (Fig. 11). Umbones often eroded; prosogyrate; nearly terminal to slightly subterminal; prodissoconch I from 100 to 110 μm in length; prodissoconch II reddish, 385 to 404 μm in length. An indistinct, raised, broadly rounded ridge or keel extends from the umbonal region to the postero-ventral margin.

External sculpture lacking, surface smooth except for concentric growth lines and fine ra-
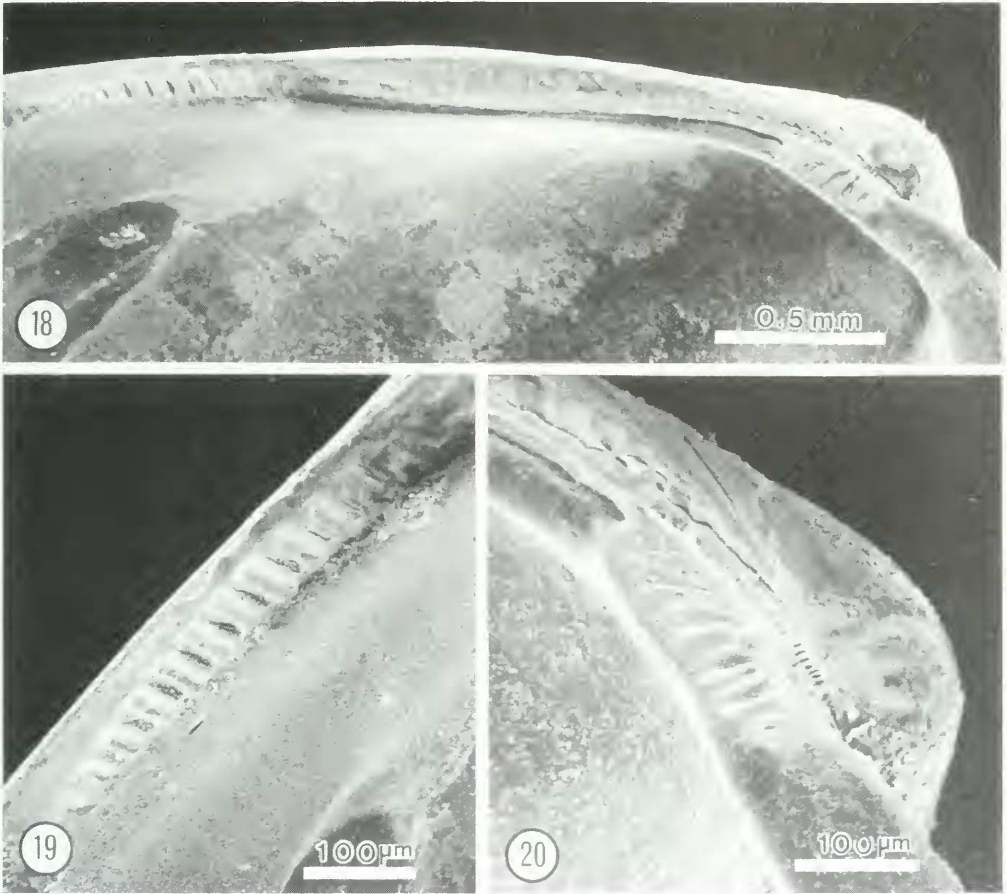
FIG. 18. "Bathymodiolus" childressi Gustafson, Turner, Lutz & Vrijenhoek. Juvenile hinge line of specimen 4.5 mm in length. Scale bar = 0.5 mm.
FIG. 19. "Bathymodiolus" childressi Gustafson, Turner, Lutz & Vrijenhoek. Hinge denticles located immediately posterior of the ligament in juvenile specimen 4.5 mm in length.
FIG. 20. "Bathymodiolus" childressi Gustafson, Turner, Lutz & Vrijenhoek. Hinge denticles located immediately below the umbo in juvenile specimen 4.5 mm in length.

dial periostracal corrugations in the median ventral area. Shell dull-white beneath a dark-brown to straw-yellow periostracum. Antero-dorsal portion of shell variably eroded depending on age and collection site. Interior off-white, predominately nacreous.

Ligament opisthodetic, parivincular, extending posteriorly from umbones to occupy 38% to 58% of dorsal margin. Adult hinge edentulous, thickened below and anterior to umbo. Juvenile hinge with 8 to 9 denticles immediately posterior to ligament and with 4 to 5 denticles located immediately below umbones (Figs. 18–20). Hinge denticles obsolete in specimens greater than 11 mm in length.

Muscle Scars: Muscle scars and pallial line indistinct. Anterior adductor scar oblong, below and posterior to the umbo; posterior adductor scar round, contiguous dorsally with single posterior byssal-pedal retractor scar; anterior retractor scar located in posterior portion of umbonal cavity; posterior byssal retractors forming continuous scar extending from directly beneath posterior end of ligament to antero-dorsal edge of posterior adductor scar (Fig. 12). Ventral pallial line straight, well

inset, paralleling the ventral shell margin and extending from postero-ventral edge of anterior adductor scar to posterior adductor.

Selected measurements (in mm):

length	height	width	anterior length	Dive	
88.7	46.1	37.7	—	JSL 3129	Holotype ANSP
83.3	43.3	29.6	1.1	JSL 3129	Paratype MNHN
73.4	39.5	30.0	3.8	JSL 3129	Paratype ANSP
67.6	36.5	29.3	2.6	JSL 3129	Paratype Rutgers
86.1	44.3	36.5	2.1	JSL 3137	Paratype HMNS
123.6	58.4	46.0	4.5	JSL 3145	Paratype USNM
118.5	53.3	46.0	2.4	JSL 3145	Paratype MCZ
45.9	23.4	20.5	0.2	A 2211	Paratype HMNS
56.7	30.2	25.2	1.3	A 2211	Paratype Rutgers
63.5	32.6	28.6	2.7	A 2211	Paratype ANSP
106.8	48.9	41.5	2.3	JSL 3145	Paratype USNM
94.1	45.5	39.4	4.2	JSL 3137	Paratype Rutgers
78.4	39.6	28.5	1.5	JSL 3129	Paratype HMNS
90.6	45.5	37.6	2.5	JSL 3137	Paratype MNHN
61.4	30.7	28.1	1.1	JSL 3137	Paratype MNHN

Internal Morphology

Musculature: Although the posterior byssal retractors form one continuous muscle scar in each valve (see description above, Fig. 12), posterior byssal retractors are subdivided into six main muscle bundles (Fig. 13). Posterior pedal retractors small, thin, arising from antero-dorsal portion of the foot mass and passing lateral to anterior bundle of posterior byssal retractors. Siphonal retractors not evident. Anterior retractors arising just ventral to origin of anterior portion of posterior byssal retractors on dorsal surface of byssal-pedal mass and passing anteriorly to insert in posterior portion of umbonal cavity (Fig. 13). Paired labial palp suspensors slender, extending forward as branches of anterior retractors to attach just behind and adjacent to anterior adductor. Posterior adductor oblong; anterior adductor small, round in cross-section.

Foot and Byssus: Foot thick; shape in preserved specimens variable, dependent on degree of contraction. Byssal strands light-to-dark-brown, wide, flat, unornamented. Byssal gland extending down foot behind byssal groove.

Mantle and Mantle Cavity: Connections between edge of ascending lamellae and surface of mantle lobes and visceral mass weak or lacking, resulting in incomplete separation of incurrent and excurrent chambers. Lacking muscular longitudinal ridges for attachment of ascending lamellae to mantle lobes and visceral mass (see Kenk & Wilson, 1985: 260). Ventral edges of inner mantle lobes thickened and muscular. In life, excurrent tubuliform siphon capable of moderate extension beyond end of shell. Lacking horizontal branchial septum between incurrent and excurrent chambers; incurrent and excurrent chambers not physically separated posterior to the posterior adductor. Posterior end of gill axes attach to inner wall of fused inner mantle lobes just ventral to excurrent siphon. Short valvular siphonal membrane joins right and left lobes, extending anteriorly a short distance into pedal gape; anterior edge of valvular siphonal membrane smooth, lacking central papilla. Pedo-byssal gape extensive; incurrent aperture extending from anterior end of valvular siphonal membrane to posterior edge of anterior adductor.

Ctenidia: Demibranchs approximately equal-sized, tall, fleshy; ventral margins with well-developed food grooves; dorsal food grooves in deep folds just below the junction between the ascending lamellae and both the mantle lobes and the visceral mass. Ctenidia off-white; filaments thin for the group examined in this report, but broader than typical for mytilids. Distal interlamellar junctions lacking; descending and ascending portion of each filament connected apically to one-quarter height of demibranch; every 2nd to 6th filament is a "principal filament" (see Atkins, 1937: text fig. 18, type B[1b]) exhibiting short interlamellar septum extending dorsally to a slight degree. Lacking "tubular connections" (see Kenk & Wilson, 1985) between free edges of ascending lamellae and gill axes.

Labial Palps: Paired labial palps greatly modified from the typical filter-feeding type, appearing to function as sorting area for material gathered by the foot rather than the

ctenidia. Base of inner and outer palp pair widely separated. Inner pair placed farther posteriorly, large and muscular with long proboscid-like extension of far posterior end. Mouth situated at basal mid-point of anterior end of inner pair of labial palps, farther posterior than typical for mytilids. Outer pair of palps more anterior, triangular, muscular, but smaller than inner pair with shorter proboscid-like extension.

Digestive System: Stomach and direct intestine situated left of the mid-line; rectum on mid-line posterior to entry into ventricle. Intestine leaves posterior end of stomach and traverses a short distance posteriorly to the left of the mid-line; intestine/rectum with a very short recurrent loop, which turns in a clockwise direction when viewed dorsally, just prior to turning upwards to enter the ventral aspect of the ventricle just posterior to the auricular ostia.

Remarks: "Bathymodiolus" childressi possesses a combination of morphological characters not seen in any previously described deep-sea mytilid genus; however, genetic distance measures (Nei's D and percent sequence divergence for 246 bp of the mtDNA COI gene) do not clearly separate this species from other members of the genus Bathymodiolus. So as to avoid erecting a new mono-specific genus, this species is provisionally placed in Bathymodiolus. Specimens of "Bathymodiolus" childressi previously designated Seep Mytilid Ia (Louisiana Continental Slope) and Ib (Alamiños Canyon) appear identical in all particulars and are here regarded as conspecific.

"Bathymodiolus" childressi differs from all other species referred to Bathymodiolus in having multiple separation of the posterior byssal retractors (similar to what is seen in Modiolus), a single posterior byssal retractor scar, and a rectum that enters the ventricle posterior to the level of the auricular ostia. "Bathymodiolus" childressi differs from B. heckerae and B. brooksi in having a more anteriorly located umbo, a recurrent intestinal loop, and lacking a papilla on the valvular siphonal membrane. "Bathymodiolus" childressi differs from all other Bathymodiolus species, except B. platifrons, in having the umbo located at the extreme anterior end of the shell, in an almost terminal position. Although superficially similar to B. platifrons, "Bathymodiolus" childressi differs from B.

platifrons in having a single posterior byssal retractor scar, a rectum that enters the ventricle posterior to the level of the auricular ostia, a recurrent intestine, and lacking a papilla on the valvular siphonal membrane (Hashimoto & Okutani, 1994).

The protein electrophoretic study of Craddock et al. (1995) showed that "Bathymodiolus" childressi (designated as AC/Ib and BH/Ia) and B. heckerae (designated as FL/Va) had pairwise Nei's D values of 2.086 and 2.188, whereas comparison of these two populations of "Bathymodiolus" childressi with B. brooksi (designated as AC/II) yielded D values of 1.531 and 1.507, respectively. Pairwise comparison of the two "Bathymodiolus" childressi populations and B. thermophilus (designated as MB/Bt) yielded Nei's D values of 1.831 and 1.833 (Craddock et al., 1995; Table 8). These genetic distances straddle the range of values for species-level separation and are not sufficient evidence to support erection of a new genus for "Bathymodiolus" childressi.

The two populations of "Bathymodiolus" childressi were more highly divergent in pairwise comparisons with T. fisheri (D = 2.209 and 2.138), and "Idas" macdonaldi (D = 2.656 and 2.570) (Table 8; Craddock et al., 1995). Since most congeneric groupings of animals have Nei's D values less than 2.0 (Nei, 1987), these results support generic separation of T. fisheri and "Idas" macdonaldi from "Bathymodiolus" childressi

Analysis of a 246 bp region of the mtDNA COI gene showed a sequence divergence of 17.6% to 18.7% between "Bathymodiolus" childressi and B. heckerae, and 17.2% between "Bathymodiolus" childressi and B. brooksi (Table 8; W. R. Hoeh, unpublished data). Sequence divergence between "Bathymodiolus" childressi and T. fisheri ranged from 47.9% to 48.7%. Similar values for "Bathymodiolus" childressi and "Idas" macdonaldi ranged from 43.4% to 45.0% (Table 8). These levels of mtDNA divergence support separate species status for "Bathymodiolus" childressi, and separation at the generic level from T. fisheri and "Idas" macdonaldi.

"Bathymodiolus" childressi occurs over a depth range of at least 1670 m, which is not remarkable considering that Knudsen (1970) recorded at least 15 abyssal and hadal bivalves with depth ranges greater than 2000 m and numerous other deep-sea bivalves with similar or greater vertical distributions are on record (references in Allen, 1983).

"Bathymodiolus" childressi from both the Louisiana Continental Slope and Alamiños Canyon contain methanotrophic symbionts in their gills (Fisher, 1993), which provide a source of carbon and energy to the host mussel via oxidation of environmental methane (Childress et al., 1986; Fisher et al., 1987). Intracellular bacteria are limited to bacteriocytes within the gill filaments and have internal membrane structures typical of Type I methanotrophs (Childress et al., 1986; Fisher et al., 1987). Analysis of 16S rRNA gene sequence data reveals the presence of only a single bacterial species in "Bathymodiolus" childressi (Cavanaugh, 1992).

The labial palp suspensors of "Bathymodiolus" childressi provide support for the large labial palps. Although rare in the Mytilidae in general, similar muscles occur in the deep sea mytilids Dacrydium ockelmanni Mattson & Warén, 1977 (mislabelled "pedobyssal retractors"), D. angulare Ockelmann, 1983 ("labial palp suspensors") and B. thermophilus ("labial palp muscles") (Kenk & Wilson, 1985), as well as in B. heckerae and B. brooksi described in this report.

The fine scale distribution of "Bathymodiolus" childressi at hydrocarbon/brine seeps on the Louisiana Continental Slope is significantly correlated with methane concentration (MacDonald et al., 1989). Living mussels occur in clusters near gas vents, around areas of general fluid discharge where seeping brine may be a carrier of methane (MacDonald et al., 1989, 1990a), and around brine-filled depressions on the sea-floor where the density of brine (up to 3.5 times normal seawater) traps methane in close proximity to oxygen laden seawater (MacDonald et al., 1990c). Although "Bathymodiolus" childressi form discrete beds on soft sediments and among carbonate outcrops, they also occur on and among clumps of the vestimentiferan tubeworm Lamellibrachia sp. (MacDonald et al., 1989). Two other species of mussel, T. fisheri and "Idas" macdonaldi co-occur with "Bathymodiolus" childressi at some sites on the Louisiana Continental Slope, but they are far less common and were only recently recognized (Fisher & Childress, 1992; I. R. MacDonald, pers. comm.). Other fauna associated with "Bathymodiolus" childressi at Louisiana Continental Slope sites include the trochid gastropod Cataegis meroglypta McLean & Quinn, 1987; the nerite gastropod Bathynerita naticoidea Clarke, 1989; the shrimp Alvinocaris stactophila Williams, 1988; and the crabs Rochinia crassa (A. Milne Edwards, 1879), Benthochascon schmitti Rathbun, 1931, and Munidopsis sp. (MacDonald et al., 1989, 1990a, c).

Published information on communities at Alamiños Canyon are scanty but we know that "Bathymodiolus" childressi shares this site with the mussel B. brooksi, vestimentiferan tubeworms, galatheid crabs, and swarms of white shrimp.

Numerous, round, white-rimmed, egg capsule scars (or the egg capsules themselves) are often found on the posterior and posterodorsal portion of the shell of "Bathymodiolus" childressi from Bush Hill, Green Canyon, and Brine Pool NR-1. These capsules are deposited by Bathynerita naticoidea (C. R. Fisher, pers. comm.).

Micrographs depicting the prodissoconchs I and II of "Bathymodiolus" childressi have been published in Gustafson & Lutz (1994: figs. 4.1, 4.2). The prodissoconch I length of 100 to 110 μm, the prodissoconch II length of 385 to 404 μm and the sculpture of concentric growth lines on the prodissoconch II are consistent with characteristics indicative of planktotrophic development (Gustafson & Lutz, 1994).

Etymology: The specific name honors Dr. James J. Childress, University of California - Santa Barbara, whose seminal work on the physiology of this species revealed its reliance on a methane-based symbiosis with intracellular bacteria (Childress et al., 1986). The working designation "Seep Mytilid Ia" was given to this species from the Louisiana seeps and "Seep Mytilid Ib" to members of this species from Alamiños Canyon.

Range: Known from the northern Gulf of Mexico on the Louisiana Continental Slope in 546 to 737 m and from the western Gulf of Mexico at Alamiños Canyon in 2222 m (Table 5).

Tamu Gustafson, Turner, Lutz & Vrijenhoek, new genus

Type species: Tamu fisheri Gustafson, Turner, Lutz & Vrijenhoek, new species.

Description: Shell smooth, modioliform, with sub-terminal umbones; adult hinge edentulous, juvenile hinge with small denticulations anterior and posterior to ligament; posterior retractors divided into anterior and posterior portions, posterior retractor scars separate; small pedal retractors present; mantle open ventrally; demibranchs of ctenidia hypertro-

phied and fleshy, filaments broadly thickened, with well-developed ventral food grooves; symbiotic bacteria associated with external gill surfaces; intestine with a short recurrent loop beneath the ventricle, rectum entering ventricle anterior to the auricular ostia.

Remarks: Tamu possesses a combination of morphological characteristics not seen in any existing mytilid genus (Table 9) and exhibits genetic distance measures (Nei's D and percent sequence divergence for 246 bp of the mtDNA COI gene) that clearly separate the type species from the genus Bathymodiolus (Table 8). Comparison of Tamu with existing genera is hampered by the fact that most deep-sea mytilid genera have been described without benefit of anatomical studies; in many cases, surviving type specimens consist of shell material only. Tamu differs from Bathymodiolus in having thickened gills that contain symbiotic bacteria in "pockets," open to the mantle cavity; by its relatively small size; and by the absence of palp suspensors. Tamu differs from Idas and Adipicola in having posterior byssal retractors that are divided into anterior and posterior portions and in loosing the hinge denticulations at maturity. Tamu further differs from Idas (as represented by putative I. argenteus, the type species, and I. washingtonia) in having thickened versus filamentous gills, lateral versus medial placement of the pedal retractors (relative to the posterior byssal retractors), and outer and inner demibranchs of equal length. Tamu further differs from Adipicola (as represented by Adipicola sp. from the Middle Valley hydrothermal vent site on the Juan de Fuca Ridge in the northwest Pacific) in having separate pedal retractors that are not integrated with the posterior byssal retractors. Tamu differs from other deep-sea mytilid genera (Amygdalum, Benthomodiolus, and Dacrydium) in having thickened ctenidia versus filamentous ctenidia. In addition, the outer demibranchs are only one half the length of the inner demibranchs in Benthomodiolus and Dacrydium, whereas outer and inner demibranchs are of equal size in Tamu. Palp suspensors are absent in Tamu, but present in both Benthomodiolus (type species) and Dacrydium (Ockelmann, 1983).

Nei's genetic distance based on 26 allozyme loci between T. fisheri and members of the genus Bathymodiolus, ranged from 1.983 to 3.305 (Craddock et al. 1995; Table 8). These Nei's D values are outside the range of those for most congeneric groupings of animals (Nei, 1987). Percent sequence divergence for a 246 bp region of the mtDNA COI gene ranged from 47.9% to 52.2% between T. fisheri and members of the genus Bathymodiolus. Tamu fisheri and "Idas" macdonaldi were somewhat closer related, with a pairwise Nei's D value of 1.859 and a COI sequence divergence of 38% (Table 8).

The generic name derives from the abbreviation for Texas A & M University (TAMU). Members of the Geochemical and Environmental Research Group at Texas A & M University have been instrumental in the discovery and exploration of numerous hydrocarbon/brine seeps on the Louisiana and Texas Continental Slope where many of these mussel taxa were first discovered.

Tamu fisheri Gustafson, Turner, Lutz & Vrijenhoek, new species
Figures 11–13, 21–23

This species, known since 1991, has been referred to in literature concerning seep and vent biology but was never formally described. The following is a list of these references.

"Seep mytilid III" – Fisher, 1993: 609.
"Seep mytilid III" – Gustafson & Lutz, 1994: 81, fig. 4.3 [micrograph of prodissoconch II].
"GB/III" – Craddock et al., 1995: 479–483.
"Seep mytilid III" – Nelson & Fisher, 1995: table 3.
"Seep mytilid III" – Kochevar & Childress, 1996: tables 1, 2.

Types: Holotype ANSP A18849 from JOHNSON SEA-LINK-I Dive 3108 at Bush Hill hydrocarbon seep at 27°46.91′N; 91°30.36′W, 210 km south southwest of Grand Isle, Louisiana in 548 m. The type-locality is between Blocks 184 and 185 in the Green Canyon offshore petroleum leasing area in the Gulf of Mexico on the Louisiana Continental Slope. Five paratypes (ANSP 400780, 400781; USNM, MCZ) are from the same dive and locality. Additional paratypes are from JOHNSON SEA-LINK-I Dives 3131 and 3149 at approximately 27°50′N; 91°10′W in 701 and 650 m, respectively (ANSP 400782; MCZ, HMNS).

Shell Morphology: Shell small, length no greater than 60 mm. Modioliform, thick and sturdy, essentially equivalve. Anterior margin

TABLE 9. Comparison of morphological characters among genera of deep-sea mytilid mussels.

Character/Genus	Adipicola[1]	Amygdalum	Bathymodiolus (type species)	Benthomodiolus (type species)	Dacrydium	Idas[2]	Modiolus	Tamu (type species)
Maximum shell length	36 mm	44 mm	160 mm	18 mm	4 mm	9 mm	230 mm	54 mm
Hinge denticulations	retained in some species	?	juvenile only	absent	retained in adult	retained in adult	?	juvenile only
Ventral mantle fusion	absent	absent	extensive[3]	absent	absent	absent	absent	absent
Posterior byssal retractors	undivided	separate	separate	separate	undivided	undivided	multiple muscle bundles, single scar	separate
Pedal retractors	absent	absent	present	present	absent	present	present	present
Palp suspensors	?	?	present	present	present	absent	absent	absent
Intestine	?	?	straight	1 short recurrent loop	1 recurrent loop	1 recurrent loop	2 recurrent loops	1 recurrent loop
Entry point of rectum into ventricle	?	?	anterior to auricular ostia	anterior to auricular ostia	anterior to auricular ostia	anterior to auricular ostia	?	anterior to auricular ostia
Ctenidia	thickened	filamentous	thickened, endosymbiotic bacteria	filamentous	filamentous	filamentous	filamentous	thickened, ectosymbiotic bacteria
Outer demibranchs	equal with inner demibranchs	?	equal with inner demibranchs	1/2 length of inner demibranchs	1/2 length of inner demibranchs	1/2 length of inner demibranchs	equal with inner demibranchs	equal with inner demibranchs

[1]Based on Adipicola sp. from Middle Valley on the Juan de Fuca Ridge.
[2]Based on Idas argenteus from the Tongue of the Ocean (TOTO) site and I. washingtonia from South Cleft hydrothermal vent on the Juan de Fuca Ridge off southern British Columbia and from whale bone in the Santa Catalina Basin off southern California.
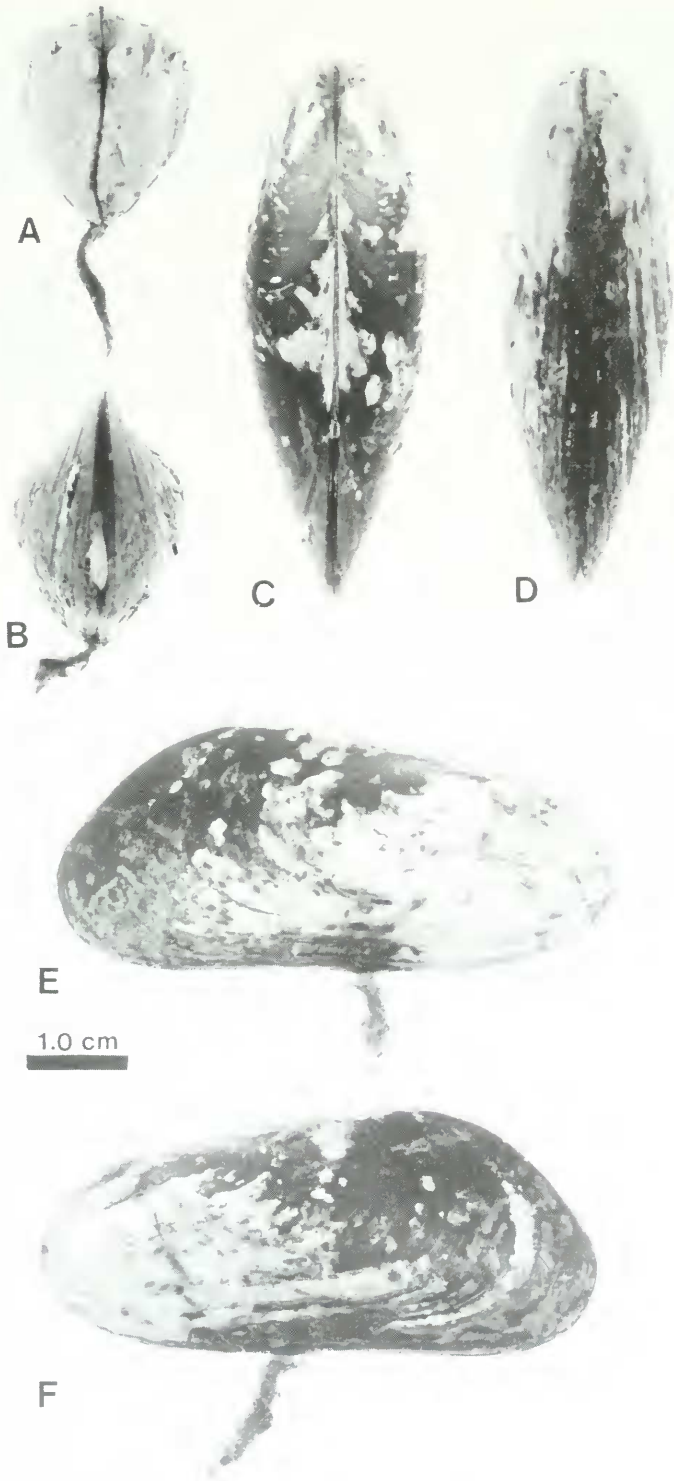[3]Character present in type species only, absent in other members of Bathymodiolus.

FIG. 21. Tamu fisheri Gustafson, Turner, Lutz & Vrijenhoek. Holotype, ANSP A18849. A, anterior view; B, posterior view; C, dorsal view; D, ventral view; E, lateral view of right valve; F, lateral view of left valve.
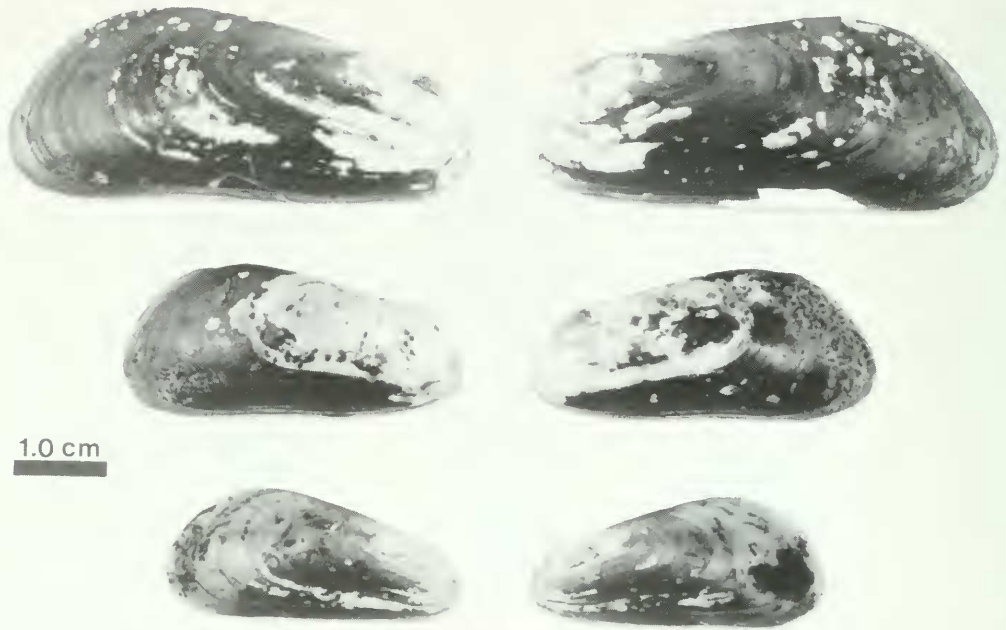
FIG. 22. Tamu fisheri Gustafson, Turner, Lutz & Vrijenhoek. External views of a growth series of shells illustrating ontogenetic change in shape.

FIG. 23. Tamu fisheri Gustafson, Turner, Lutz & Vrijenhoek. Remnants of juvenile hinge denticles located immediately posterior of the ligament in juvenile specimen 16.9 mm in length.

sharply rounded; posterior margin broadly rounded, becoming angular dorsally; ventral margin straight, very slightly concave in region of byssal gape in largest specimens; dorsal margin very broadly convex (Figs. 11, 12, 21, 22). Shell length greater than twice the height. Umbones often eroded; prosogyrate; subterminal, positioned within the anterior one-twentieth. Prodissoconch II red, 460 μm in length. A raised, broadly rounded ridge extends from the umbonal ridge to the posterior-ventral margin.

External sculpture lacking, surface smooth except for concentric growth lines and very fine radial periostracal corrugations in the median ventral area. Shell dull-white beneath dark-brown to straw-yellow periostracum. Antero-dorsal portion of periostracum and shell variably eroded depending on age and collection site. Interior polished, off-white, predominately nacreous.

Ligament opisthodetic, parivincular, extending posteriorly from the umbones to occupy from 37% to 50% of the dorsal margin. Adult hinge edentulous, thickened below and anterior to the umbo. Juvenile hinge with denticles immediately posterior of the ligament and immediately below the umbones (Fig. 23). Hinge denticles obsolete in specimens greater than 17 mm in length.

Muscle Scars: Anterior adductor scar oblong, positioned at an oblique angle near the antero-ventral margin, below the umbo. Posterior adductor scar round, contiguous with small siphonal retractor scar ventrally and posterior portion of posterior byssal-pedal retractor scar dorsally. Anterior retractor scar located within upper extremity of umbonal cavity directly beneath umbo. Posterior byssal retractors form two scars with a moderate gap between them; anterior scar obliquely elliptical, directly beneath the posterior end of the ligament, poste-

rior scar elliptical, parallel to the antero-posterior axis of the shell and located antero-dorsally to and bordering the posterior adductor scar (Fig. 12). Ventral pallial line prominent, extending from the median posterior aspect of the anterior adductor scar to the posterior adductor, curving slightly upwards and then downwards to form an indentation in the byssal gape region at about the mid-point of the antero-posterior axis; small siphonal retractor scar located at posterior end of ventral pallial line contiguous with posterior adductor.

Measurements (in mm):

length	height	width	anterior length	Dive	
53.5	23.8	17.6	—	JSL 3108	Holotype ANSP
46.8	21.4	16.2	2.2	JSL 3108	Paratype Rutgers
50.0	21.9	17.0	2.8	JSL 3108	Paratype USNM
51.4	21.0	18.5	1.9	JSL 3108	Paratype ANSP
48.8	20.6	16.1	2.2	JSL 3108	Paratype ANSP
49.6	20.5	16.2	2.0	JSL 3108	Paratype USNM
31.6	14.1	10.1	2.0	JSL 3149	Paratype HMNS
33.9	15.2	12.3	2.0	JSL 3149	Paratype Rutgers
33.9	15.9	10.6	1.7	JSL 3149	Paratype MCZ
37.0	16.3	13.3	2.9	JSL 3149	Paratype ANSP

Internal Morphology

Musculature: Main features of musculature evident from previous description of muscle scars and Figure 13. Posterior byssal retractors separated into posterior and anterior portions, each consisting of two main muscle bundles, that attach separately to the shell; the posterior portion inserting along the postero-dorsal edge of the posterior adductor and the anterior portion inserting just below and posterior to the posterior end of the ligament. Pedal retractors very slender, arising from antero-dorsal portion of foot, passing lateral to the anterior retractors and inserting lateral to posterior portion of the posterior byssal retractors. Siphonal retractors indistinct, originating in inner mantle margin around the excurrent siphon and attaching along postero-ventral edge of the posterior adductor. Anterior retractors arising from dorso-lateral portion of the foot mass and passing anteriorly to insert in the antero-dorsal extremity of the umbonal cavity. Labial palp suspensors not evident. Posterior and anterior adductor rounded.

Foot and Byssus: Foot long, thick; shape in preserved specimens variable, dependent on degree of contraction. Byssal strands few to profuse, gray to light-brown, thin, flat, unornamented. Byssal gland extending down foot behind byssal groove, without extension dorsal to origin of anterior retractors.

Mantle and Mantle Cavity: Connections between edge of ascending lamellae and surface of mantle lobes and visceral mass weak or lacking, resulting in incomplete separation of incurrent and excurrent chambers. Lacking muscular longitudinal ridges for attachment of ascending lamellae to mantle lobes and visceral mass (see Kenk & Wilson, 1985: 260). Ventral edges of inner mantle lobes not thickened and muscular. Excurrent siphonal opening small, tubuliform siphon capable of moderate extension beyond perimeter of shell, lacking internal diaphragm. Fusion of inner mantle immediately below excurrent siphon forms short, incomplete, horizontal branchial septum between incurrent and excurrent chambers; incurrent and excurrent chambers not completely separated posterior of posterior adductor; posterior ends of gill axes attach to underside of horizontal branchial septum. Short valvular siphonal membrane joins right and left lobes, extending anteriorly a short distance into pedal gape; anterior edge of valvular siphonal membrane smooth, lacking central papilla. Pedo-byssal gape extensive; incurrent aperture extending from anterior end of valvular siphonal membrane to posterior edge of anterior adductor.

Ctenidia: Lamellae of unequal height; ascending lamellae two-thirds height of descending, resulting in inner and outer demibranchs forming short-armed W-shaped gill when viewed in cross-section. Demibranchs unequal in length; inner demibranch slightly longer anteriorly than outer. Demibranchs hypertrophied, thick, short; ventral edges have well-developed, recessed food grooves; dorsal food grooves present in deep folds just below junction of ascending lamellae and areas of attachment to mantle lobes and visceral mass. Filaments broad, moderately fleshy; ctenidia and filaments white. Distal interlamellar junctions lacking; lamellae joined apically to approximately one-half height of descending and three-quarter height of ascending lamellae; "principal filaments" (see Atkins, 1937: text fig. 18, type B[1b]) lacking.

TABLE 10. Means (mm) and standard errors (in parentheses) of mensural characters in five new species of seep mytilids from the Gulf of Mexico. N = sample size; L = shell length; H = shell height; W = width of shell valves; A = anterior length; and G = ligament length (see Fig. 2).

Species	Site	N	L	H	W	A	G
Bathymodiolus heckerae	West Florida Escarpment	236	90.6 (2.8)	31.2 (0.8)	24.2 (0.6)	10.7 (0.4)	38.0 (1.2)
Bathymodiolus brooksi	Alamiños Canyon	75	115.1 (3.5)	46.1 (1.2)	34.7 (1.0)	8.3 (0.3)	58.8 (1.8)
Bathymodiolus brooksi	West Florida Escarpment	5	100.0 (9.6)	40.4 (4.1)	29.9 (2.7)	5.8 (0.9)	40.7 (6.1)
"Bathymodiolus" childressi	Alamiños Canyon	29	54.7 (1.3)	29.5 (0.8)	24.3 (0.7)	1.5 (0.1)	27.5 (0.8)
"Bathymodiolus" childressi	Bush Hill	91	78.6 (0.9)	40.2 (0.4)	32.2 (0.4)	2.5 (0.1)	36.1 (0.5)
"Bathymodiolus" childressi	Brine Pool NR-1	27	107.7 (3.1)	50.1 (1.2)	40.7 (1.3)	3.6 (0.2)	49.7 (1.5)
Tamu fisheri	Bush Hill	13	37.9 (3.2)	16.7 (1.3)	13.0 (1.1)	2.1 (0.1)	18.0 (1.7)
"Idas" macdonaldi	Garden Banks-386	5	11.8 (0.9)	5.8 (0.5)	6.0 (0.4)	0.6 (0.1)	4.1 (0.4)

Lacking "tubular connections" (see Kenk & Wilson, 1985) between free edges of ascending lamellae and gill axes.

Labial Palps: Paired labial palps short, broad, flat, triangular; inner surfaces plicate, outer surfaces smooth; bases of inner and outer pair coincident; both pairs in normal anterior position, without proboscid-like extensions. Outer pair of palps larger, up to twice the size of inner pair. Mouth situated normally, at the basal junction of inner and outer palps. Extreme anterior portions of gill placed between inner and outer palps coincident with plicate palp surfaces.

Digestive System: Alimentary system well developed for the group; stomach and direct intestine located on body mid-line. Intestine leaves posterior end of stomach and passes posteriorly down midline ventral to ventricle; short recurrent loop to the right begins immediately below posterior end of ventricle; recurrent intestine passes anteriorly on right side. Rectum turns to the mid-line and enters extreme antero-ventral portion of ventricle anterior to the auricular openings.

Remarks: Some characters that separate T. fisheri and other deep-sea mytilids have been previously discussed in the remarks section for the genus description. The small adult size of T. fisheri and the bifurcation of both posterior and anterior portions of the posterior byssal retractors further differentiate this species from "Bathymodiolus" childressi, B. brooksi, and B. heckerae. Conversely, T. fish-

eri is much larger than the largest specimens of "Idas" macdonaldi (Table 10). Tamu fisheri has a short recurrent intestinal loop similar to "Bathymodiolus" childressi, but in contrast to the straight intestine present in most species of Bathymodiolus.

Tamu fisheri is rare at both Bush Hill and the site near Garden Banks, in contrast to the much more abundant "Bathymodiolus" childressi. Fauna associated with T. fisheri at Bush Hill are discussed in the remarks section for "Bathymodiolus" childressi. The site near Garden Banks is "extremely oily," but lacking in "major community development (stunted tube worms, isolated bivalves)" (I. R. MacDonald, pers. comm.). The new mussel "Idas" macdonaldi is also found at the site near Garden Banks. Tamu fisheri has an association with sulfur-oxidizing symbiotic bacteria on the surface of the gills (C. R. Fisher, pers. comm.). These bacteria express high activities of the enzyme ribulose biphosphate carboxylase/ oxygenase. Two specimens of T. fisheri, including the holotype, contained an unidentified commensal polynoid polychaete within the mantle cavity.

Round, white-rimmed, egg capsule scars identical to those commonly deposited by the snail Bathynerita naticoidea on the shell of "Bathymodiolus" childressi (C. R. Fisher, pers. comm.) were found on the postero-dorsal portion of one shell of T. fisheri from Bush Hill. Gustafson & Lutz (1994: fig. 4.3) illustrate the prodissoconch II of T. fisheri (designated "Seep Mytilid III") with a length of approximately 460 μm, and a surface sculpture of

concentric growth lines alone, which is consistent with characteristics indicative of planktotrophic development.

Etymology: The specific name honors Dr. Charles R. Fisher of The Pennsylvania State University, who has provided us with many of the specimens examined in this report and who has done a great deal of the seminal work on the physiology of these symbiotic mussel taxa. The working designation "Seep Mytilid III" was given to this species from the Louisiana Continental Slope cold-water seeps.

Range: Known only from hydrocarbon seeps at Bush Hill in Green Canyon and from a site within Garden Banks petroleum lease block 386 on the Louisiana Continental Slope in the northern Gulf of Mexico in depths from 546 to 650 m (Table 6).

Subfamily Modiolinae
Type genus: Modiolus Lamarck, 1799

Idas Jeffreys, 1876
Idas Jeffreys, 1876: 428 (type species, by monotype, Idas argenteus Jeffreys, 1876, non Idas Mulsant, 1876).
Idasola Iredale, 1915: 340 (unnecessary replacement name for Idas Jeffreys, 1876: 428, non Mulsant, 1876 [Warén, 1991: 116]).
(For further synonymy, see Dell 1987:25).

Revised Diagnosis: Shell small (8 to 22 mm maximum length), modioliform, rhomboidal to oblong, smooth, umbones subterminal; periostracum light-yellow to brownish-yellow; prodissoconch reddish-brown; ligament extending along most of postero-dorsal margin; fine hinge denticulations present anterior and posterior to ligament. Posterior retractors undivided; posterior retractor scars continuous with posterior adductor scar. Separate pedal retractors present. All of the species assigned to this genus occur in deep-water and are commonly collected in association with sunken organic matter, including wood, whale bone, and fish skeletons.

Remarks: Warén (1991: 116) presented convincing evidence, based on the requirements of the ICZN, for the maintenance of Jeffrey's name Idas in contrast to the replacement name Idasola of Iredale (1915). Warén (1991) also synonymized Idas and Adipicola, stating that he could not see why Dell (1987) distinguished between these two genera. Warén (1991: 116) presumed that Dell based his generic distinction on the presence or absence of "crenulated areas along the hinge line," which Warén (1991) considered to be a juvenile character, lost with growth in adult Adipicola but retained in adult Idas due to the latter's smaller size at maturity. In support of Warén's (1991) position, hinge denticulations were also present in all juvenile specimens of the species described in this report, being retained only in adult "Idas" macdonaldi, the smallest species examined. However, Dell (1987) also pointed out that in Idas the pedal retractor is associated with the posterior byssal retractor, whereas there is no sign of a separate pedal retractor in Adipicola.

Other anatomical differences have not been studied in the type specimens of these genera (type specimens consist of shells only); however, analyses for this report of the anatomy in putative I. argenteus (the type species of the genus), I. washingtonia, and Adipicola sp. (see Materials and Methods section for source material) revealed further differences between these two genera. Specimens of I. argenteus and I. washingtonia have outer demibranchs that are only one-half the length of the inner demibranchs, whereas specimens of Adipicola sp. have outer demibranchs equal in size to the inner demibranchs. In addition, Adipicola sp. have thick fleshy gills, whereas specimens of I. argenteus and I. washingtonia have thin, filamentous gills and "Idas" macdonaldi have moderately thickened but still essentially filamentous gills. These anatomical observations argue against placing Idas and Adipicola in synonymy.

Idas differs from Bathymodiolus, Benthomodiolus, and Tamu in having undivided posterior byssal retractors (Dell, 1987), medial versus lateral placement of the pedal retractors (relative to the position of the posterior byssal retractors), and hinge denticulations anterior and posterior of the ligament in adult specimens. Idas further differs from Bathymodiolus and Tamu in its small adult size and in having thin filamentous ctenidia, the outer demibranchs of which are only one-half the length of the inner demibranchs (as exemplified by I. argenteus and I. washingtonia). Idas further differs from Bathymodiolus in lacking palp suspensors (as exemplified by I. argenteus, I. washingtonia, and "Idas" macdonaldi).

Idas differs from Dacrydium in having sepa-

rate posterior pedal retractors (in I. argenteus, I. washingtonia, and "Idas" macdonaldi), umbones located some distance from the anterior end, and in lacking palp suspensors.

"Idas" macdonaldi Gustafson, Turner, Lutz & Vrijenhoek, new species
Figures 11–13, 24–27

Types: Holotype ANSP A18850 from JOHNSON SEA-LINK-I Dive 3149 at 27°50'N; 92°10'W, in 650 m in the Gulf of Mexico on the Louisiana Continental Slope near Garden Banks block 386 offshore petroleum leasing area. Two paratypes (ANSP 400783, 400784) and 6 additional specimens (Rutgers) are from the same dive and locality.

Shell Morphology: Shell small, less than 15 mm long, modioliform, sturdy and stout, translucent, essentially equivalve. Anterior margin sharply rounded; posterior margin broadly rounded; ventral margin straight but with concave indentation in region of byssal gape, indentation more pronounced in longest specimens; dorsal margin broadly convex, more or less straight over the span of the ligament (Figs. 11, 12, 24). Umbones often eroded; prosogyrate; subterminal, positioned within anterior one-twentieth. Raised, broadly rounded external ridge extends from umbonal region to posterior-ventral margin.

   External sculpture lacking, surface smooth except for concentric growth lines. Shell dull-white beneath straw-yellow periostracum. Antero-dorsal portion of periostracum variably eroded, periostracum sometimes lacking on dorsal three-quarters. Interior off-white, predominately nacreous.

   Ligament opisthodetic, parivincular, extending posteriorly from the umbones to occupy from 31% to 37% of dorsal margin. Adult hinge thickened below and anterior to umbones, with 12 to 28 denticles immediately posterior to ligament and 9 to 19 denticles immediately below umbones on a thickened boss (Figs. 25–27).

Muscle Scars: Muscle scars and pallial line indistinct. Anterior adductor scar round, somewhat truncated posteriorly, positioned near antero-ventral margin, below umbo. Posterior adductor scar round, contiguous with posterior byssal-pedal retractor scar dorsally. Anterior byssal retractor scar located within upper extremity of umbonal cavity directly beneath umbo. Elongated posterior byssal-pedal re-

tractor scar not divided; parallel to antero-posterior axis of shell; posterior end of muscle scar bordering posterior adductor scar antero-dorsally, anterior end terminating below posterior hinge denticles (Fig. 12). Ventral pallial line straight without dorsal concavity, extending from postero-ventral aspect of anterior adductor scar to postero-ventral edge of posterior adductor.

Measurements (in mm):

length	height	width	anterior length	Dive	
10.6	4.9	5.1	—	JSL 3149	Holotype ANSP
9.9	4.8	4.5	—	JSL 3149	Paratype ANSP
11.2	5.3	4.8	—	JSL 3149	Paratype ANSP
9.9	5.0	5.3	0.7	JSL 3149	Specimen Rutgers
11.2	5.4	5.6	0.5	JSL 3149	Specimen MCZ
13.4	5.8	6.2	0.8	JSL 3149	Specimen Rutgers
6.6	3.7	3.3	—	JSL 3149	Specimen Rutgers
8.4	4.0	3.6	—	JSL 3149	Specimen USNM
8.2	4.3	3.8	—	JSL 3149	Specimen HMNS

Internal Morphology

Musculature: Main features of musculature evident from previous description of muscle scars and Figure 13. Posterior byssal retractors continuous, not divided into posterior and anterior portions; attaching to shell from antero-dorsal edge of posterior adductor to just posterior of and below ligament's posterior end. Separate pedal retractors located medially, between posterior byssal retractors, partially obscured when viewed from a lateral aspect; becoming integrated with posterior byssal retractors at point of shell attachment. Anterior retractors arising from dorso-lateral aspects of foot mass and extending anteriorly to attach to shell in antero-dorsal extremity of umbonal cavity. Labial palp suspensors not evident. Posterior adductor rounded, anterior adductor slightly oblong.

Foot and Byssus: Foot thick; shape in preserved specimens variable, dependent on degree of contraction. Byssal strands white to light-brown, thin, flat, unornamented. Purple tinted byssal gland extending down foot be-
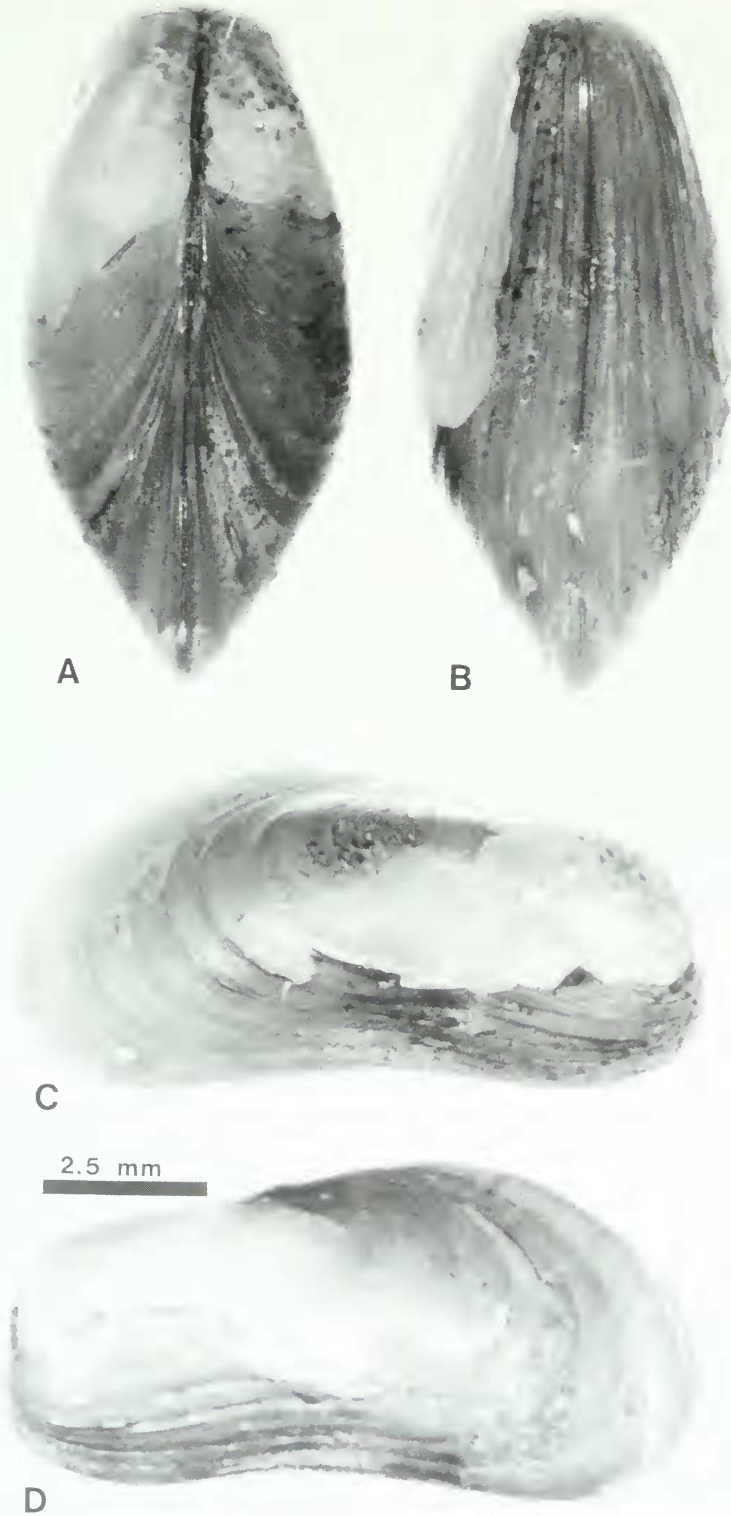
FIG. 24. "Idas" macdonaldi Gustafson, Turner, Lutz & Vrijenhoek. Holotype, ANSP A18849. A, dorsal view; B, ventral view; C, lateral view of right valve; D, lateral view of left valve.
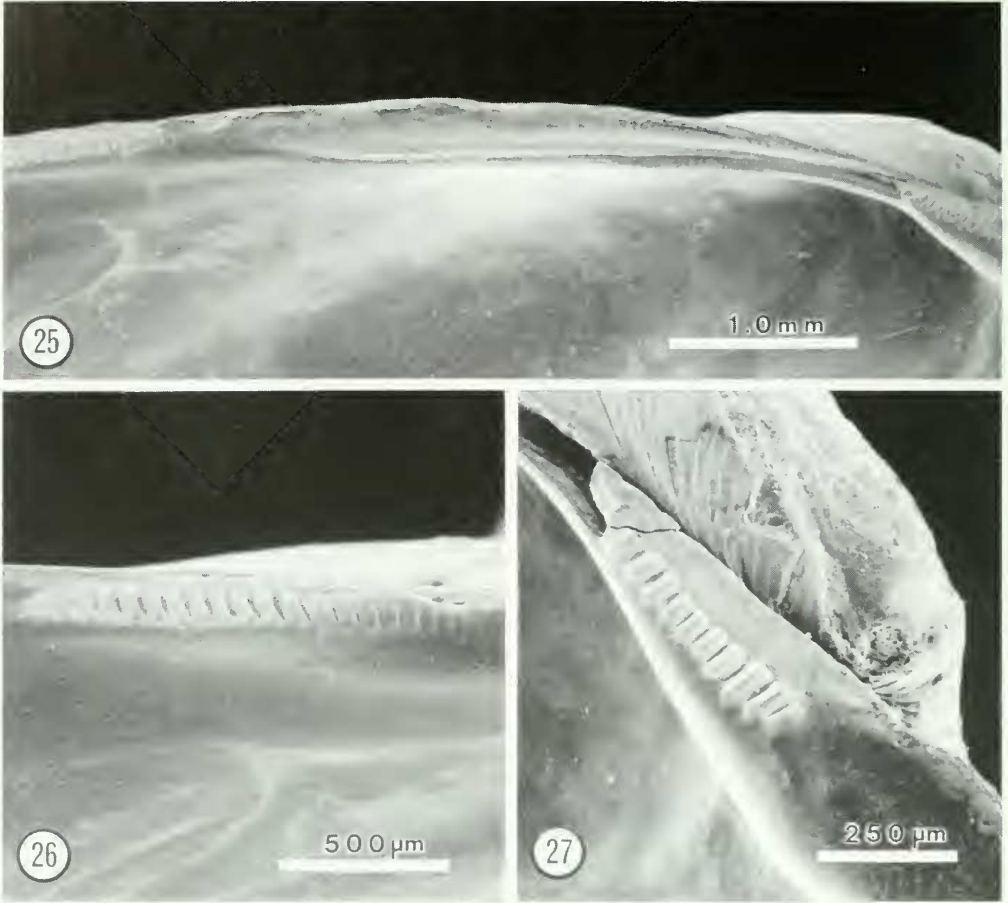
FIG. 25. "Idas" macdonaldi Gustafson, Turner, Lutz & Vrijenhoek. Juvenile hinge line of specimen 10.4 mm in length.

FIG. 26. "Idas" macdonaldi Gustafson, Turner, Lutz & Vrijenhoek. Hinge denticles located immediately posterior of the ligament in juvenile specimen 10.4 mm in length.

FIG. 27. "Idas" macdonaldi Gustafson, Turner, Lutz & Vrijenhoek. Hinge denticles located immediately below the umbo in juvenile specimen 10.4 mm in length.

hind byssal groove; extending laterally and slightly dorsal to origin of anterior retractors.

Mantle and Mantle Cavity: Connections between edge of ascending lamellae and surface of mantle lobes and visceral mass weak or lacking, resulting in incomplete separation of incurrent and excurrent chambers. Lacking muscular longitudinal ridges for attachment of ascending lamellae to mantle lobes and visceral mass (see Kenk & Wilson, 1985: 260). Ventral edges of inner mantle lobes not thickened and muscular. Excurrent siphon little more than a simple slit with short extensible collar, not capable of extension beyond perimeter of shell. Unusual internal diaphragm occludes ventral two-thirds of excurrent siphonal opening, attached dorsally to slender muscular bridge that connects side walls of internal opening approximately two-thirds of distance from the siphon floor. Lacking horizontal branchial septum; incurrent and excurrent chambers not separated posterior of posterior adductor. Posterior end of gill axes attach to inner wall of fused inner mantle lobes just ventral to exhalent siphon. Short valvular siphonal membrane joins right and left mantle lobes, extending anteriorly a short distance into pedal gape; anterior edge of valvular siphonal membrane smooth, lacking central papilla.

Pedo-byssal gape extensive; incurrent aperture extending from anterior end of valvular siphonal membrane to posterior edge of anterior adductor.

Ctenidia: Lamellae of unequal height; ascending lamellae two-thirds to three-quarters height of descending, resulting in inner and outer demibranchs forming short-armed W-shaped gill. Demibranchs unequal; outer demibranchs shorter anteriorly, approximately 90% to 95% the length of the inner demibranchs. Status of food grooves not determined due to poor preservation. Ctenidia filamentous to moderately thickened; filaments off-white in color. Distal interlamellar junctions lacking; lamellae joined apically to approximately one-third height of gill; "principal filaments" (see Atkins, 1937: text fig. 18, type B [1b]) lacking. Lacking "tubular connections" (see Kenk & Wilson, 1985) between free edges of ascending lamellae and gill axes.

Labial Palps: Paired labial palps short, thickened, broadly triangular; inner surfaces plicate, outer surfaces smooth; bases of inner and outer pair coincident; both pairs in normal anterior position, without proboscid-like extensions. Outer pair of palps larger, up to twice the size of inner pair. Mouth situated normally, at the basal junction of inner and outer palps.

Digestive System: Alimentary system well developed for group; stomach and direct intestine located slightly to left of body mid-line. Intestine leaves posterior end of stomach and passes posteriorly left of mid-line and ventral to ventricle; very short recurrent loop to the right begins before ventricle's mid-point; recurrent intestine then passes beneath ventricle to right side of mid-line and proceeds anteriorly for a short distance. Rectum then returns to mid-line and enters floor of ventricle anterior to auricular openings and about one-fifth of distance from ventricle's anterior.

Remarks: "Idas" macdonaldi possesses a combination of morphological features not seen in any described genus of mytilid mussel. So as to avoid erecting a new mono-specific genus, this species is provisionally placed in Idas. Although most morphological features place "Idas" macdonaldi in the genus Idas, the ctenidial structure is radically different from that seen in other species of this genus. In "Idas" macdonaldi, the outer demibranchs extend to 90% to 95% the length of the inner demibranchs and are moderately thickened. However, examination of adult I. argenteus (type species of Idas) collected at The Tongue of The Ocean (TOTO) in the North Atlantic, revealed filamentous outer demibranchs that are only half the length of the inner demibranchs. Long, thick outer demibranchs have not been previously reported for the genus Idas. Reduced outer demibranchs were also observed in I. washingtonia from the South Cleft hydrothermal vent site on the Juan de Fuca Ridge and in I. washingtonia from whale bone in the Santa Catalina Basin. Type specimens of I. argenteus (type material consists of shell only) and I. washingtonia were not examined for this feature.

Reduced outer demibranchs have also been observed in Dacrydium ockelmanni (Mattson & Warén, 1977) and in paratypes of Benthomodiolus abyssicola (Knudsen, 1970; see Discussion below). Other morphological characters of "Idas" macdonaldi correspond with those of the genus Idas, although specimens of "Idas" macdonaldi are larger than most other known species of this genus.

Several features of "Idas" macdonaldi serve to distinguish this species from other mussels described herein; small size, rhomboidal shape, unseparated posterior byssal retractors, and lack of palp suspensors (although the latter are also lacking in T. fisheri). No previous records of Idas or Adipicola from the Gulf of Mexico exist. Other Atlantic species of Idas and Adipicola include I. argenteus, A. simpsoni (Marshall, 1900) and A. pelagica (Woodward, 1854). Although listed as arising in the Recent geological period in Moore (1969), Idas has been recorded from the Miocene of northern Germany (Janssen, 1972; I. lignicola) and the Cretaceous of Egypt (Abbass, 1962; I. faragi and I. nakadyi).

"Idas" macdonaldi differs from I. coopingeri (Smith, 1885) (reported from deep-water sites off Australia), I. japonica (Habe, 1976) (from off Japan and New Zealand), I. argenteus, and I. washingtonia in having the umbones located in an almost terminal position; the anterior length (A) of the shell occupies the anterior 3% to 7% of the shell in "Idas" macdonaldi, the anterior 16% in I. coopingeri, the anterior 10% to 14% in I. japonica, the anterior 12% to 20% in I. argenteus, and the anterior 23% to 33% in I. washingtonia (Dell, 1987). "Idas" macdonaldi further differs from I. japonica in having a less narrow and elongate shell and in having the pedal and posterior byssal retractors almost at

TABLE 11. Correlation matrix of mensural characters ($\log_{10}$ transformed) from five new species of mytilids from the Gulf of Mexico. The PC-1 and PC-2 columns represent loadings of each character on the first two, Varimax rotated, principal component axes. PC-1 plus PC-2 explained 98.97% of the variance in these five characters. L = shell length; H = shell height; W = width of shell valves; A = anterior length; and G = ligament length.

Variable	L	H	W	A	G	PC-1	PC-2
L	1.0000	0.9425	0.9297	0.7170	0.9821	0.8507	0.5136
H		1.0000	0.9842	0.4811	0.9565	0.9670	0.2358
W			1.0000	0.4516	0.9450	0.9750	0.2043
A				1.0000	0.6497	0.2614	0.9649
G					1.0000	0.8845	0.4302

right angles to the plane of the anterior byssal retractors (the posterior and anterior retractors are essentially in the same plane in I. japonica) (Dell, 1987).

"Idas" macdonaldi differs from I. ghisottii (Warén & Carrozza, 1990), from the Mediterranean Sea, in having a more rhomboidal and less elongate shell shape and in maintaining hinge denticulations anterior of the ligament up to adult size. "Idas" macdonaldi differs from I. indica (Smith, 1904), from off the Andaman Islands, in having a smooth shell surface and more anteriorly located umbones. Myrina modiolaeformis Sturany, 1896, was placed in Idas by Dell (1987); however, Warén (1991) questioned whether this species really belongs in Idas. This species has not been found since the original description and its systematic placement is uncertain. Narrow, elongate specimens described as Idas dalli Smith, 1885, from off Culebra Island, West Indies, also apparently do not belong in Idas, according to K. W. Ockelmann, as reported in Dell (1987).

The largest paratype of "Idas" macdonaldi was found attached by byssal threads to the external shell surface of a specimen of the vesicomyid bivalve Vesicomya cordata Boss, 1968. Other specimens were "found interstitially in a mass of pea-sized carbonate rubble" (I. R. MacDonald, pers. comm.). Other fauna at this "extremely oily" site, which "lacked major community development," are T. fisheri, "Bathymodiolus" childressi, stunted tubeworms, and isolated vesicomyid bivalves (I. R. MacDonald, pers. comm.). Two specimens of "Idas" macdonaldi contained a single large unidentified polynoid polychaete within the mantle cavity. These polynoids have been forwarded to Dr. James Blake for taxonomic description.

Etymology: The specific name honors Dr. Ian R. MacDonald of the Geochemical and Environmental Research Group at Texas A & M University, who is responsible for the collection, preservation, and forwarding of this new species. The working designation "Seep Mytilid IV" was given to this species from the Louisiana Continental Slope cold-water seeps.

Range: Known only from the northern Gulf of Mexico on the Louisiana Continental Slope in the vicinity of Garden Banks block 386 offshore petroleum leasing area in 650 m (Table 7).

MORPHOMETRIC ANALYSIS

The new mytilid species fall into three discrete size classes (Table 10). The two Bathymodiolus species and "Bathymodiolus" childressi were generally large, although differences in size existed among samples within two of the species. Tamu fisheri was intermediate in size and "Idas" macdonaldi was small. Principle components analyses proceeded from a correlation matrix (Table 11) of the five characters illustrated in Figure 2. The first principal components axis (PCI) represented covariates of overall size (L, W, H, and G). Length of the shell anterior to the beak (character A) loaded highly on PC2.

The five species of mussels separated reasonably well according to the PCI and PC2 axes (Fig. 29). The two Bathymodiolus species found at the West Florida Escarpment site, although similar in size, can be discriminated because the anterior length (A) of B. heckerae is proportionally larger than in B. brooksi. Similarly, B. brooksi and "Bathymodiolus" childressi at the Alamiños Canyon site can be discriminated because the anterior length (A) of B. brooksi is greater than in "Bathymodiolus" childressi, at a given size. Adult specimens of the three species found along the Louisiana Continental Slope sites can be discriminated easily because of their non-
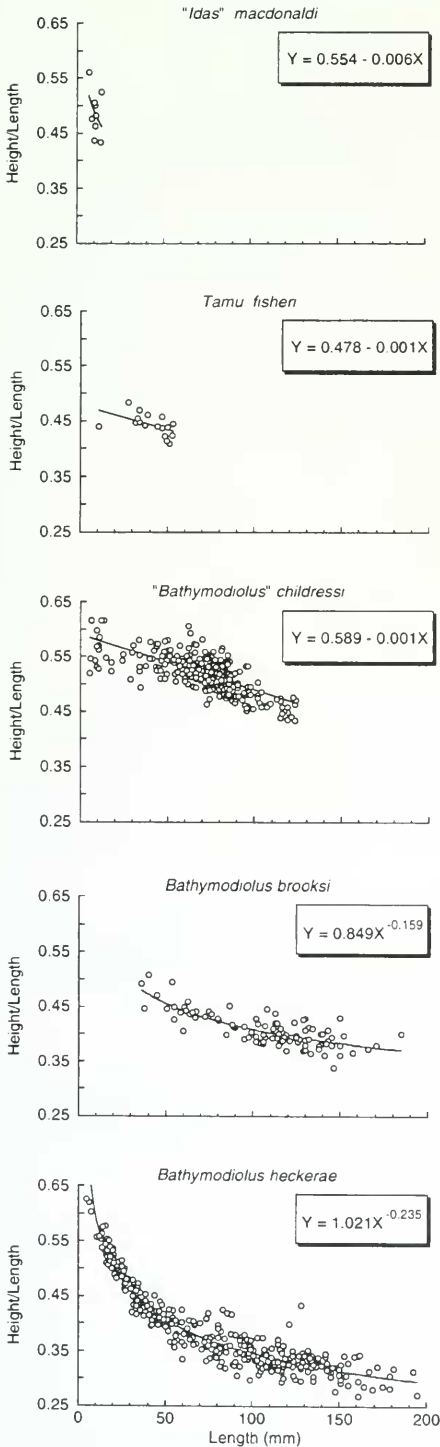
FIG. 28. Plots of the ratio of height to length against length for *"Idas" macdonaldi, Tamu fisheri, "Bathymodiolus" childressi, Bathymodiolus brooksi,* and *Bathymodiolus heckerae.*

specimens of the three species found along the Louisiana Continental Slope sites can be discriminated easily because of their non-overlapping size distributions; *"Bathymodiolus" childressi* being largest, *T. fisheri* being intermediate, and *"Idas" macdonaldi* being smallest (Table 10).

DISCUSSION

Prior to the discovery of the species described in this study, mytilid mussel genera with representatives in the deep sea (defined as those whose range extends below 600 m) included *Adipicola, Amygdalum, Bathymodiolus, Benthomodiolus, Crenella, Dacrydium, Idas, Modiolus,* and *Musculus* (Clarke, 1962; Knudsen, 1979; Dell, 1987; Kenk & Wilson, 1985). Of these genera, only *Bathymodiolus* was known to contain endosymbiotic bacteria in specialized gill cells (Felbeck et al., 1981; Cavanaugh, 1983; Fiala-Médioni, 1984), although a mussel species retrieved from whale bone on the deep-sea floor and referred to *I. washingtonia* was reported to "host" chemoautotrophic bacteria (Smith et al., 1989), and two mussels from the Middle Valley hydrothermal vent on the northern Juan de Fuca Ridge referred to *I. washingtonia* and *Adipicola* sp. respectively, were reported to have bacteria associated with the microvillar surface of the gill cells (Juniper et al., 1992). With the exception of *"Idas" macdonaldi,* the mussel species described in this study, possess fleshy, thickened gills, similar to *B. thermophilus.* Gills of this type are thought to indicate the presence of a bacterial association (Fisher, 1990). Both *B. brooksi* and *B. heckerae* harbor two distinct populations of endosymbiotic gill bacteria (one having the morphology of a type I methanotroph and the other resembling a sulfide oxidizing bacterium); *B. thermophilus* (sulfide-oxidizing endosymbiont) and *"Bathymodiolus" childressi* (methanotrophic endosymbiont) have only one symbiont (Childress et al., 1986; Cavanaugh et al., 1987; Fisher et al., 1991; Cavanaugh, 1992; Cavanaugh et al., 1992; C. M. Cavanaugh, pers. comm.). *Tamu fisheri* apparently has an association with bacteria on the surface of the gill (C. R. Fisher, pers. comm.).

Anatomical characters used to separate the new species herein described from each other and from previously described *Bathymodiolus* species are summarized in Table 12. Cosel et al. (1994) were not able to inves-
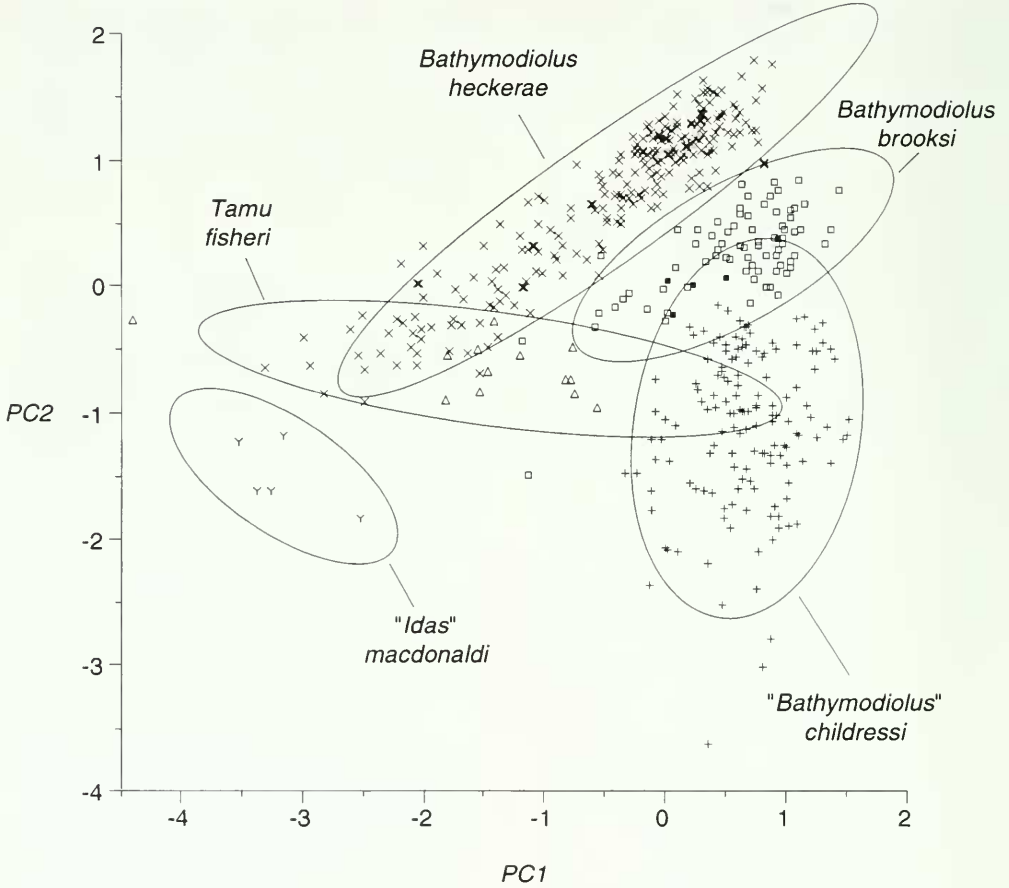
FIG. 29. Scatter plots of the first two principle components (PC1 and PC2) for shell measurements of all available specimens. Ellipses encompass 95% confidence limits for each species. Bathymodiolus heckerae = (x), Bathymodiolus brooksi (Alamiños Canyon = □; West Florida Escarpment = ■), "Bathymodiolus" childressi = (+), Tamu fisheri = (△), and "Idas"macdonaldi = (Y).

Bathymodiolus by Hashimoto & Okutani (1994) and Cosel et al., (1994), as well as the species of Bathymodiolus herein described, lack the extensive ventral mantle fusion and the prominent longitudinal muscular ridge for attachment of the ascending lamellae to the mantle, diagnostic of the type species B. thermophilus (Kenk & Wilson 1985). In most species of Bathymodiolus, the intestine is more or less straight, lacking a recurrent loop, whereas a short or very short recurrent intestinal loop is present in B. aduloides, "Bathymodiolus" childressi, T. fisheri, and "Idas" macdonaldi. The rectum enters the ventricle in "Bathymodiolus" childressi at a point posterior to the level of the auricular ostia, whereas in other Bathymodiolus species the rectum enters the ventricle at a point anterior to the level of the auricular ostia (Table 12). The posterior byssal retractors are separated into separate anterior and posterior portions in Bathymodiolus, but not in "Bathymodiolus" childressi.

The affinities of the new deep-sea mytilid taxa described herein to existing deep-sea mytilids, including B. thermophilus, are not at all certain. The genera Amygdalum, Crenella, and Musculus all have typically filamentous filibranch gills and shell characters which separate them from the other genera under discussion. Modiolus also has typically filamentous gills. Relationships with Benthomodiolus, Dacrydium, and Adipicola are more problematical. Major anatomical characters of these deep-sea genera are summarized in Table 9.

Recently, the validity of two primary diag-

TABLE 12. Comparison of morphological characters among previously described species of Bathymodiolus and new mytilid mussel species described herein. Morphological characters are numbered 1–13 and character states are explained below. Dash (–) indicates data were unavailable.

Species\Character	1	2	3	4	5	6	7	8	9	10	11	12	13
B. thermophilus	1	1	1	1	1	0	0	1	0	0.42–0.57	0.32–0.50	0.05–0.09	184
B. japonicus	0	–	1	–	–	0	0	0	–	0.51–0.63	0.34–0.49	–	106
B. platifrons	0	–	1	–	1	0	0	1	–	0.50–0.68	0.34–0.47	–	115
B. aduloides	0	–	1	–	1	0	1	0	–	0.41–0.52	0.30–0.37	–	96
B. septemdierum	0	–	1	1	1	0	0	0	–	0.43–0.66	0.29–0.46	–	124
B. brevior	0	–	1	1	–	–	0	0	–	0.45–0.61	0.36–0.45	–	143
B. elongatus	0	–	1	1	–	–	2	0	–	0.37–0.56	0.35–0.44	–	156
B. puteoserpentis	0	–	1	1	1	0	0	1	0	0.49–0.62	0.38–0.52	–	119
B. heckerae	0	0	1	1	1	0	0	1	–	0.27–0.63	0.20–0.41	0.06–0.16	192
B. brooksi	0	0	1	1	1	1	0	1	–	0.34–0.51	0.25–0.35	0.03–0.10	185
"B." childressi	0	0	2	0	1	1	1	0	0	0.43–0.62	0.33–0.51	0.00–0.06	124
Tamu fisheri	0	0	1	0	0	0	0	0	0	0.41–0.48	0.28–0.37	0.04–0.13	54
"Idas" macdonaldi	0	0	0	2	0	0	1	0	1	0.43–0.56	0.43–0.54	0.03–0.07	14

Morphological characters and character states
(1) Mid-ventral mantle fusion: 0 = absent; 1 = present.
(2) Muscular longitudinal ridge on mantle surface at attachment point of dorsal edges of ascending lamellae: 0 = absent; 1 = present.
(3) Separation of posterior byssal retractors into anterior and posterior portions: 0 = unseparated, single muscle scar; 1 = widely separated, separate muscle scars; 2 = multiple separation, single muscle scar.
(4) Pedal retractor muscles: 0 = thin, reduced; 1 = prominent; 2 = medial to pedo-byssal retractors.
(5) Palp suspensor muscles: 0 = absent; 1 = present.
(6) Entry point of rectum into ventricle: 0 = anterior to auricular ostia; 1 = posterior to auricular ostia.
(7) Recurrent loop of intestine: 0 = absent; 1 = single loop; 2 = double loop.
(8) Central papilla on anterior rim of valvular siphonal membrane: 0 = absent; 1 = present.
(9) Hinge denticulations: 0 = present in juvenile only; 1 = retained in adult.
(10) Height/length.
(11) Width/length.
(12) Anterior length/length.
(13) Maximum length (mm).

nostic characters that have been used to separate the smaller of these deep-sea mytilid taxa, the presence or absence of "periostracal hairs" and "vertical hinge striations," have come under question. The so-called periostracal hairs considered by some to be a diagnostic character of Idas, Benthomodiolus (Dell, 1987), and some other mytilids may not be of periostracal origin (Bottjer & Carter, 1980), but may merely be byssal gland secretions laid down over the exterior of the normal periostracum by the foot, as suggested by Ockelmann (1983). A scanning electron microscopic examination of "periostracal hairs" on small specimens of several species described herein suggests that the hairs on the surface of these shells are of byssal origin. Likewise, the vertical hinge denticles, thought to be a diagnostic character of Idas and of some Adipicola (Dell, 1987), are a character common to most juvenile modioliform mussels. These hinge denticulations are maintained in adult Idas and in some species of Adipicola as a consequence of their small size (Warén, 1991). In the present study, small specimens of every species examined had hinge denticles both in front of and behind the hinge ligament. With the exception of "Idas" macdonaldi, these denticles were absent in adult specimens.

We have examined paratypes, on loan from the Zoologisk Museum, University of Copenhagen, of Benthomodiolus abyssicola (Knudsen, 1970), the type species of Benthomodiolus. Although the intestine has a short recurrent loop and the posterior retractors are divided in this small mussel (17.2 mm maximum length) from 3270 to 3670 m in the Gulf of Panama, there are no hinge denticulations even in the smallest specimens, the gills are thin and filamentous as in typical filter-feeders, and the outer demibranchs are incomplete, extending forward only to the middle of the inner demibranchs. These characters lead us to reject a close relationship between Benthomodiolus and the five new species described herein. Kenk & Wilson (1985) came to the same conclusion concerning a relationship between Benthomodiolus and Bathymodiolus.

The genus Dacrydium consists of small (about 5 mm maximum size) "nest-building" neotenous deep-sea mussels that lack separate pedal retractors, but have reduced outer demibranchs, unseparated posterior retractors, a long recurrent intestinal loop, labial palp suspensors, and provincular and juvenile

hinge teeth that persist throughout the animal's life (Mattson & Warén, 1977; Ockelmann, 1983). This combination of characters, although similar in some respects, distinguishes Dacrydium from the five new species described herein.

Several species of small deep-sea mussels referred to the genus Modiolus (Verco, 1908; Pelseneer, 1911; Prashad, 1932) may ultimately be placed in one or the other of the above discussed genera. Recently, Modiolus willapaensis Squires & Goedert, 1991, was described from Late Eocene deposits representing ancient subduction-related methane seeps in southwestern Washington, USA (Goedert & Squires, 1990; Squires & Goedert, 1991). This species apparently did not obtain lengths greater than 27 mm. Although superficially resembling seep mussels described in this study, no internal features of the shell (hinge denticulations or muscle scars) were observed in the articulated fossils and therefore relationship of M. willapaensis with extant seep mussels cannot be determined. Similarly, fossil M. exbrocchii exbrocchii Sacco have been described from Miocene (Tortonian) deposits in Italy, in association with other mollusks, such as Lucina, characteristic of seep environments (Moroni, 1966).

Although some anatomical features of B. heckerae and B. brooksi (extensive ventral pedo-byssal gape and lack of muscular attachment ridge for ascending lamellae), "Bathymodiolus" childressi (multiple posterior byssal retractors, short recurrent loop of intestine and position of rectum relative to the ventricle) and "Idas" macdonaldi (complete outer demibranchs and relatively large size) differ from that seen in the respective type species of these genera, we hesitate in erecting additional deep-sea mytilid genera for these species. On the other hand, the level of genetic divergence (Craddock et al., 1995) and the unique combination of anatomical features in T. fisheri (bifurcate posterior and anterior portions of the posterior byssal retractors, short recurrent loop of intestine, and lack of palp suspensors) argue for generic level differentiation of this species.

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APPENDIX 1

The ID#, location and museum catalog numbers of the mussel holotypes and paratypes. The holotypes and a series of paratypes are deposited in the Academy of Natural Sciences of Philadelphia (ANSP). Additional paratypes are deposited in the following institutions: United States National Museum of Natural History, Washington, D.C. (USNM): Museum of Comparative Zoology, Harvard University (MCZ); Houston Museum of Natural Science, Houston, Texas (HMNS), Museum National d'Histoire Naturelle, Paris (MNHN), and Rutgers University (RU). MNHN and RU do not assign catalog numbers to their collections.

Bathymodiolus heckerae

ID #	Location	Cat. #
A 1343	Holotype ANSP	A18846
A 1754-3	Paratype USNM	880270
A 1755-13	Paratype MCZ	316977
A 2196-8	Paratype HMNS	45307
A 2196	Paratype MNHN	
A 2196-1	Paratype RU	
A 2196-40	Paratype MNHN	
A 2197-33	Paratype HMNS	45306
A 2542-40	Paratype ANSP	400773
A 2542	Paratype ANSP	400771
A 2196	Paratype ANSP	40072
A 2196-17	Paratype HMNS	45299
A 2196-56	Paratype RU	
A 2542-13	Paratype MNHN	

Bathymodiolus booksi

ID #	Location	Cat. #
A 2211	Holotype ANSP	A18847
A 2211-13	Paratype MCZ	319676
A 2211-7	Paratype USNM	88-268
A 2211-22	Paratype MNHN	
A 2211	Paratype ANSP	400775
A 2209-11	Paratype MCZ	316973
A 2209-20	Paratype MCZ	316975
A 2209-14	Paratype MCZ	316974
A 2209	Paratype ANSP	400774
A 2209-2	Paratype RU	
A 2211-6	Paratype MNHN	
A 2209-9	Paratype RU	
A 2209-18	Paratype HMNS	45300
A 2211-36	Paratype RU	
A 2196	Paratype ANSP	400777
A 2542-7	Paratype USNM	880269
A 2542-60	Paratype HMNS	84302
A 2542	Paratype ANSP	40076

"Bathymodiolus" childressi

ID #	Location	Cat. #
JSL 3129	Holotype ANSP	A18848
JSL 3129	Paratype MNHN	
JSL 3129	Paratype ANSP	400778
JSL 3129-61	Paratype RU	
JSL 3137-39	Paratype HMNS	45303
JSL 3145-41	Paratype USNM	880272
JSL 3145-23	Paratype MCZ	316978
A 2211-39	Paratype HMNS	45308
A 2211-44	Paratype RU	
A 2211	Paratype ANSP	400779
JSL 3145-37	Paratype USNM	880271

JSL 3137-27	Paratype RU	
JSL 3129-112	Paratype HMNS	45305
JSL 3137	Paratype MNHN	
JSL 3137	Paratype MNHN	

Tamu fisheri

ID #	Location	Cat. #
JSL 3108	Holotype ANSP	A18849
JSL 3108-1	Paratype MCZ	
JSL 3108-3	Paratype USNM	880273
JSL 3108	Paratype ANSP	400780
JSL 3108	Paratype ANSP	400781
JSL 3108-11	Paratype USNM	880274
JSL 3149-1.3	Paratype HMNS	316979
JSL 3149-3.3	Paratype RU	

| JSL 3149-4.3 | Paratype MCZ | 45301 |
| JSL 3149 | Paratype ANSP | 400782 |

"Idas" macdonaldi

ID #	Location	Cat. #
JSL 3149	Holotype ANSP	A18850
JSL 3149	Paratype ANSP	400784
JSL 3149-11.6	Paratype ANSP	400783
JSL 3149-12.2	Paratype RU	
JSL 3149-12.3	Paratype MCZ	316980
JSL 3149-12.4	Paratype RU	
JSL 3149	Paratype RU	
JSL 3149-11.2	Paratype USNM	880275
JSL 3149-11.6	Paratype HMNS	45304